The Evolution of Locomotory Mode in the Lizard Genus *Niveoscincus*

An Ecomorphological Analysis of Ecology, Behaviour, Morphology and Performance Ability

Jane Melville, BSc. (Hons.)

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School of Zoology

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Abstract

I have investigated the evolution of locomotory mode in the lizard genus *Niveoscincus*, through the use of comparative phylogenetic techniques. Particular attention was paid to the morphological, locomotory, and behavioural inter-relationships in the eight species of *Niveoscincus*. The genus provides a rare opportunity to examine evolutionary processes and patterns in reptiles from temperate climates; it is located within a relatively small geographical area, and contains a limited number of species that have radiated morphologically, ecologically and behaviourally, while retaining close phylogenetic affinities. Three phylogenetically distinct ecomorphs have been identified: ground-dwelling; semi-arboreal; and saxicolous. The ground-dwelling species have relatively short limbs and long inter-limb lengths. The ability to climb appears to have evolved in the semi-arboreal species, and has involved a decrease in body size and an increase in leg length. The saxicolous species have evolved the ability to jump, with an increase in relative leg length. However, there are two distinct behavioural types within the saxicolous species: the heath/rock-dwelling and the saxicolous specialist species. Performance ability, morphology and behaviour correlate with the microhabitats in which each species lives.

This thesis is divided into a number of chapters which examine the phylogenetic relationships, microhabitat use, locomotory behaviour, performance abilities and morphological characteristics within *Niveoscincus*. The final chapter is a comparative analysis which examines the evolution of locomotory mode.

A phylogenetic analysis of data gained from sequencing the mitochondrial gene cytochrome *b* indicated that *Niveoscincus* is a monophyletic genus, which probably

speciated 5-7 m.y.a. The 8 species and 25 populations studied exhibited a non random selection of microhabitats and a preference for a particular set of environmental factors. Microhabitat selection was shown to be related to vegetation and substrate characteristics. This study also indicated that there are significant differences between the ecomorph-types in *Niveoscincus* in terms of locomotory behaviour although, as mentioned above, it is possible to divide the saxicolous group into two further ecomorph-types. Significant differences were also found in the performance abilities between the three basic ecomorph-types. The saxicolous species had high sprinting and jumping abilities, while the arboreal species were shown to be fast climbers.

The hindfoot/femur (HFT/FEL) ratio in *Niveoscincus* was higher in the faster running species, while the arboreal species were shown to have short bodies and relatively long rear legs, which could be attributed to a relatively long femur.

The comparative phylogenetic analysis indicated that there is a trade-off between sprinting/jumping and climbing in *Niveoscincus*. Species which climbed rapidly were not able to jump long distances or sprint quickly. This was not a result of differences in relative leg length, rather it was a result of behavioural factors.

This study has emphasised the importance of behaviour in the ecomorphological paradigm developed by Arnold (1983). This was achieved through quantitative estimates of the relationships between measurements of ecologically relevant performance capabilities and different morphological, habitat and behavioural traits within a group of closely related organisms. These enabled a number of important issues in ecomorphology to be addressed: (1) the interspecific relationship between morphology and a number of performance traits in *Niveoscincus*; (2) the possible trade-off between different modes of locomotion; and (3) the co-evolution of performance, morphology, behaviour, and microhabitat occupation.

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CHAPTER ONE
GENERAL INTRODUCTION

1.1 Introduction

A large part of organismic biology over the centuries has been devoted to the study of adaptation. Since Darwin, it has generally been accepted that adaptation is driven by natural selection (Harvey and Pagel, 1991). In conjunction with this there has also been much interest in the evolution of body shape and the functional significance of different morphological characteristics within an animal's environment. This area of research was formalised by Van der Klaauw (1948) who coined the term "ecological morphology". He defined this as the study of the relationships between the morphology of an organism and its environment. This is still the most common definition in use (eg. Alexander, 1988; Losos, 1990; Wainwright, 1991).

The comparative method has long been the most generally employed technique for addressing questions about common patterns of evolutionary change and natural selection, but it was not until the 1970s that ecomorphology became a popular area of research. This sudden interest was associated with advances in computer technology, particularly the introduction of desktop computers, which greatly simplified the quantitative analysis of large ecological data sets. This allowed a number of early ecomorphology papers to investigate the relationship between the morphology of species and the ecological space they occupy within a community (eg. Werner, 1974; Karr and James, 1975; Gatz, 1979). Most of the issues addressed in these studies were ecological, such as how do certain morphological features cluster with environmental characteristics? Another group of researchers took a different approach. They focussed on morphology, examining the ecological consequences of anatomical differences between species (eg. Bock and von Wahlert, 1965; Bock, 1977, 1980).

During the early 1980s a number of papers suggested a link between population genetics and the mechanism of natural selection in functional morphology and physiological ecology (eg. Huey and Stevenson, 1979; Arnold, 1983). The role of organismal design in determining how an animal interacts with its environment comes about through the effect that design has on the ability of the organism to perform various tasks and behaviours. Arnold (1983) noted that morphological, performance and fitness gradients can be constructed for individuals in a population, strengthening the quantification of the connection between morphology and fitness. This study emphasised the importance of performance testing as a key component in research that seeks to link ecology to morphology.

The development of methodologies for studying ecomorphological relationships within a population from the standpoint of fitness was paralleled by the emergence of a modern comparative method (Harvey and Pagel, 1991) that focuses on phylogenetic diversity and offers a methodology for testing whether a particular feature of design may be termed an adaptation (Wainwright and Reilly, 1994). Consequently, a renewed interest in the phylogenetic aspects of evolution has emerged over the last decade, in the form of these new research techniques that attempt to strengthen our examination of adaptive hypotheses. Phylogenetic hypotheses provide our best estimate of the evolutionary history of life and provide a rigorous basis for testing hypotheses about the adaptive nature of specific features (Wainwright and Reilly, 1994). They do this by considering the effect of phylogenetic constraints on quantitative traits (eg. Gittleman, 1981; Stearns, 1983; Pagel and Harvey, 1988; Bauwens *et al.*, 1995). These studies emphasise the point that data from related taxa are not statistically independent. Consequently, phylogenetic effects will confound commonly used statistical tests of adaptation.

Much research in the area of phylogenetic aspects of adaptation has investigated the evolution of life history traits (Brooks and McLennan, 1991). For example, correlations of mass, life history traits and phylogeny have been examined in a number

of mammal taxa (Gittleman, 1981, 1985; Stearns, 1983; Gittleman and Kot, 1990). Similar studies of various lizard taxa have also been published (eg. Dunham and Miles, 1985; Huey and Bennett, 1987; Dunham *et al.*, 1988). They have all shown that phylogenetic relationships strongly influence life history traits that had previously been assigned high adaptive significance (Brooks and McLennan, 1991). This has helped us realise that most traits of a species are inherited from its ancestors and any hypothesis examining the origins of a particular trait must encompass the phyletic transition during which the trait evolved.

More recent phylogenetic studies have incorporated aspects of the morphology/performance/fitness paradigm to examine different areas of co-evolution (eg. Martins and Garland, 1991; Garland *et al.*, 1992; Bauwens *et al.*, 1995). Comparative biologists have also taken an increased interest in behavioural evolution. Behavioural characters are again being used to generate phylogenies, a return to earlier days in ethology when phylogenetic studies of behaviour were common (Lauder and Reilly, 1996). Behavioural traits have been correlated with other characters, such as body size, territory size and brain size, to clarify phylogenetic patterns of character co-evolution (Pagel and Harvey, 1988; Brooks and McLennan, 1991; Harvey and Pagel, 1991). Many of these comparative studies are now using the phylogenetic statistical methods that have recently become available (eg. Cheverud *et al.*, 1985; Felsenstein, 1985; Bell, 1989; Grafen, 1989, 1992; Harvey and Pagel, 1991; Lynch, 1991). These studies have highlighted the integral role that behaviour plays in the study of ecomorphology.

The comparative phylogenetic studies of the last decade have shown that evolution can be investigated at more that one level. A distinction between microevolution and macroevolution was first made by Goldschmidt (1940) who proposed that there were two different evolutionary mechanisms at work. He believed that microevolution encompassed processes such as natural selection and genetic mutations which operated at a population level to produce differences within species (Brooks and McLennan,

1991). Macroevolution involved the production of new species through chromosomal mutations, regardless of the effects of natural selection. However, a new perspective has recently emerged, as a result of the current methodologies in phylogenetic systematics. This new view is based on the idea that evolution results from a variety of interacting processes, known as "forces" or "constraints", operating at different temporal and spatial scales (Brooks and McLennan, 1991). Evolutionary processes that occur at rates fast enough to manifest as changes within a single species are included in microevolutionary processes. Evolution which occurs at a slower rate, resulting in between-species patterns, is considered to be in the realm of macroevolution. Thus, microevolution and macroevolution are believed to be parts of a larger whole represented by the hierarchical nature of biological systems. Macroevolution is not autonomous from nor reducible to microevolution (Brooks and McLennan, 1991). Thus, for robust evolutionary explanations to specific questions, data from both sources are needed.

An appropriate evolutionary ecomorphological analysis requires a group that has radiated to produce species that differ in morphology, ecology, and behaviour, that is amenable to behavioural and ecological field studies and for which phylogenetic relationships are relatively well understood (Losos, 1990). This thesis examines 8 species and 15 populations of the lizard genus *Niveoscincus* (Scincidae).

1.2 Study Species

The island state of Tasmania forms the most southerly projection of the Australian continent and its cool to cold temperate climate supports a relatively impoverished reptilian fauna (Heatwole, 1976). This fauna is composed of 18 lizard species and three snake species. Until recently, the majority of the lizard species were placed in the genus *Leiolopisma* (Wilson and Knowles, 1988), but this genus has recently been recognised as polyphyletic. Hutchinson *et al.* (1990) revised the genus in a major

taxonomic and genetic study. The largest lizard genus recognised in Tasmania currently is *Niveoscincus*, or the "snow skinks". This is a genus of small to medium sized lygosomine skinks. Six species of *Niveoscincus* are endemic to Tasmania: *N. greeni, N. microlepidotus, N. ocellatus, N. orocryptus, N. palfreymani,* and *N. pretiosus.* The distribution of *N. metallicus*, on the other hand, extends from Tasmania into southern Victoria. *Niveoscincus coventryi* is the only species which is found on the australian mainland but not in Tasmania. It is restricted to south-eastern Victoria. This study incorporates all of the species and an outgroup species from the closely related genus *Pseudemoia.*

Psuedemoia was also previously included in the genus *Leiolopisma* but was reclassified by Hutchinson *et al.* (1990). The species used as an outgroup to *Niveoscincus* is *P. entrecasteauxii*, the "grass" or "tussock" skink. This species is common throughout Tasmania and its distribution extends into Victoria.

Despite the recent taxonomic revisions, little published literature on any ecological, physiological, morphological or behavioural aspects of the genus *Niveoscincus* is currently available. The most extensive report on the ecology and biogeography of Tasmanian lizards was provided by Rawlinson (1974); his work still stands as the only detailed examination of biogeography, distribution and taxonomy. However, this report is now outdated, as it predates the revised classification of *Niveoscincus.*

A number of new species, such as *N. orocryptus*, have been described since Rawlinson (1974). *Niveoscincus microlepidotus* has also been recently redescribed (Hutchinson *et al.*, 1989). Previously it was included in the species *N. pretiosus*. *Niveoscincus microlepidotus* and *N. orocryptus*, along with *N. greeni*, are the three truly alpine species found in Tasmania. Published literature on these species is restricted to a generalised description of distributions (Hutchinson *et al.*, 1989; Hutchinson and Schwaner, 1991) and two ecology/behavioural papers (Melville and Swain, 1997a,b). These species have been described as alpine lizards occurring in disjunct populations

on mountain tops above 1000 m in southern Tasmania (*N. microlepidotus*), western Tasmania (*N. orocryptus*) and north-eastern and central Tasmania (*N. greeni*) (Hutchinson and Schwaner, 1991). *Niveoscincus microlepidotus* and *N. greeni* appear to occur above the tree-line only and are restricted to more open areas, particularly dolerite boulder fields. *Niveoscincus orocryptus*, on the other hand, is reported to be restricted to the tree-line in some areas, such as Mt Eliza, but occurs above this point in other areas, such as Mt Hartz (pers. obs.).

The metallic skink, *N. metallicus*, is a better known species. Its general ecology and distribution have been described by Rawlinson (1974). This ground-dwelling species has a wide distribution and occurs in many habitats over a broad altitudinal range, from dry sclerophyll woodlands to sub-alpine heaths. The environmental disturbance associated with development appears to have benefited this species and it is commonly found in suburban gardens and in vegetation along roadsides. Despite its wide distribution, very little work has been undertaken on the species. Some thermoregulatory data have been incorporated into larger studies (Bennett and John-Alder, 1986) and there are a number of recent papers dealing with reproductive physiology (Swain and Jones, 1994, 1997a,b; Jones and Swain, 1996; Jones *et al.*, 1997).

The other two ground-dwelling species considered in this thesis, *N. coventryi* and *P. entrecasteauxii*, have been little studied. *Niveoscincus coventryi* is a cryptic lizard found in tall highland forests in Victoria. It occurs in the thick layers of bark and leaf litter (Webb, 1985). *Psuedemoia entrecasteauxii* is a grassland skink which is also very cryptic in nature. It can be found in dry sclerophyll woodlands in central and eastern Tasmania (pers. obs.). Both these species have been incorporated into larger studies of thermoregulation and general ecology (Webb, 1985; Bennett and John-Alder, 1986) but no detailed ecological data are available.

The remaining two species which have been investigated in this thesis are the arboreal lizard *N. pretiosus* and the saxicolous species *N. ocellatus*. *Niveoscincus pretiosus* is a small and agile skink which occurs throughout Tasmania, up to an altitude of 1000 m (tree-line). It is found mainly on fallen branches and trunks which form breaks in the forest canopy. However, in western Tasmania it is also found to be saxicolous in some areas. I have observed large numbers of *N. pretiosus* basking on cobbles on a beach in south-western Tasmania. *Niveoscincus ocellatus* is the largest species of *Niveoscincus* on mainland Tasmania and occurs on rocky outcrops in eastern, central and northern Tasmania. There is a very large intraspecific range in body size in this species. Populations at higher altitudes (up to 1000 m) are almost one third larger than the populations at sea level (Wapstra pers. comm.). Very little work has been completed on either of these species, although Wapstra and Swain (1996) examined the feeding ecology of *N. ocellatus*.

The remaining species of *Niveoscincus* is *N. palfreymani* (the Pedra Branca skink); this is the only endangered Tasmanian reptile. Because of its status live specimens were unavailable for this study and only preserved specimens for genetic work could be used. This is the largest species of *Niveoscincus,* with snout-vent lengths of up to 90 mm. This species consists of a single population living on a rocky islet (Pedra Branca) 26 km off the south west coast of Tasmania. In 1997 the population had dropped from around 500 animals to about 200 (Brothers, pers comm.). Pedra Branca is a barren windswept island with no vegetation. The lizards feed on fish dropped or regurgitated by the bird colonies. Consequently, the lizard population is dependent on the wellbeing of the bird colony. Although little has been published on this species a monitoring programme has been maintained on the bird and lizard populations of Pedra Branca since 1978. All lizards are toe-clipped and life-history data have been collected by the Tasmanian National Parks Service.

In terms of general biology *Niveoscincus* forms a fairly homogenous genus of closely related species. All species are active foragers (having a predominantly arthropod-

based diet), shuttling heliotherms and have diurnal activity patterns. Most of them are either primarily terrestrial, saxicolous or arboreal. A few species, such as *N. microlepidotus,* show a combination of saxicolous, ground-dwelling and arboreal behaviours. All of the species thermoregulate behaviourally by restricting activity times, altering body postures and shuttling between sun and shade. They have different, although partially overlapping, geographic distributions and habitat preferences. Despite these similarities, *Niveoscincus* has radiated sufficiently in morphology, ecology, and behaviour to make it an ideal genus for an ecomorphological study on the evolution of locomotory mode.

1.3 An Overview of this Thesis and Major Research Objectives

Ecomorphology has been an integral tool of ecologists and evolutionary biologists in elucidating patterns and interpreting processes (Ricklefs and Miles, 1994). By combining experimental and observational studies on a restricted group of closely related taxa with broadly comparative analyses, the ecomorphological approach should clarify fundamental issues in evolutionary adaptation (Ricklefs and Miles, 1994). This study combines both experimental and observational data to investigate and quantify the evolution of three modes of locomotion in *Niveoscincus*.

This thesis consists of nine chapters, the first being this introductory chapter. The second is a description of the field sites where lizards and observational data were collected. The six following chapters present my experimental results. Each component of my ecomorphological analysis is covered in a separate chapter: phylogeny (Chapter 3); ecology (Chapter 4); behaviour (Chapter 5); performance (Chapter 6); and morphology (Chapter 7). Chapter 8 brings together the data from all previous sections in a phylogenetic analysis of the evolution of locomotion in *Niveoscincus*. The final chapter of this thesis provides a general discussion, in which my findings are reviewed and future research directions are considered.

The primary aim of this thesis is to investigate the evolution of locomotory modes in *Niveoscincus*. However, there are many other areas of importance which are also examined. The complete list of objectives is presented below.

1. To establish a reliable phylogeny for the genus *Niveoscincus* using DNA sequencing (Chapter 3).
2. To quantify microhabitat occupation by the species of *Niveoscincus* and *Pseudemoia entrecasteauxii* (Chapter 4). The microhabitat separation of the species was also examined.
3. To quantify the locomotory behaviour of the study species through multivariate analysis (Chapter 5). Discriminant function analyses were also used to examine the differences in behaviour between the species.
4. To provide the first comparative investigation of ecologically relevant performance abilities in Tasmanian skinks. The performance abilities (jumping, climbing, and sprinting) of the study species were quantified under laboratory conditions (Chapter 6).
5. To conduct a comparative investigation of morphological features in *Niveoscincus* relevant to the ecology, locomotory performance and behaviour of the species studied (Chapter 7).
6. To quantify the interspecific relationships between morphology and a number of performance traits in *Niveoscincus* (Chapter 8).
7. To examine the possibility of a trade-off between different modes of locomotion in *Niveoscincus* (Chapter 8).
8. To investigate the possibility of parallel evolution in performance, morphology, behaviour, and ecology (Chapter 8). How these factors may affect the fitness of a species in its environment is discussed.
9. To attempt to quantify the relationships between an ecologically relevant performance capability and different morphological, microhabitat and behavioural traits within a group of closely related organisms (Chapter 8).

CHAPTER TWO

GENERAL MATERIALS AND METHODS

2.1 Study Sites

The island of Tasmania is separated from the southern tip of mainland Australia by Bass Strait. It is situated between 40 and 43.5° south and has a temperate maritime climate. The climate ranges from cool temperate at sea level to cold temperate in highland Tasmania. All the field sites are located in Tasmania except for one which is located in the south-eastern corner the Australian mainland. This study site is located in Victoria on the edge of the Central Highlands, northeast of Melbourne, and has a cool temperate climate.

The study sites were selected for the following reasons: (1) the presence of study species; (2) accessibility; and (3) the presence of a number of distinct microhabitats. Each field site consisted of a square area, where possible, whose sides were approximately 500 m in length. All the Tasmanian field sites are indicated on Figure 2.1.

2.1.1 Alpine Habitats

The alpine zone of Tasmania occurs approximately 1000 m asl. At this altitude no months are frost-free (Jackson, 1981) and glazing storms throughout the year affect the height and form of vegetation. Snow may fall at any time during the year, but snow lie is usually restricted to winter and early spring.

Past periglacial and glacial action has had an important role in the formation of dolerite boulder fields in the alpine zone of many mountains. Much of Tasmania has been altered by the Pleistocene glaciation period, with most glacial activity occurring on the eastern, lee side of mountains. As a result, large moraine deposits of dolerite boulders, in which, vegetative growth is limited, are common and extensive.

In Tasmania the mountains are "rock mountains", a topography that is the result of severe erosion by glacial ice during the Pleistocene ice ages and of the continuing erosion by frost after glaciation (Plate 2.1). At these high altitudes soils are often associated with periglacial solifluction activity (Ogden and Powell, 1979). Soils are often earthy brown and have a relatively coarse texture. They are generally shallow and contain boulders and rock fragments, and range from deeper clay-based soils on dolerite mountains to thin organic acidic soils. In the wetter areas there is a higher organic content, tending towards peat.

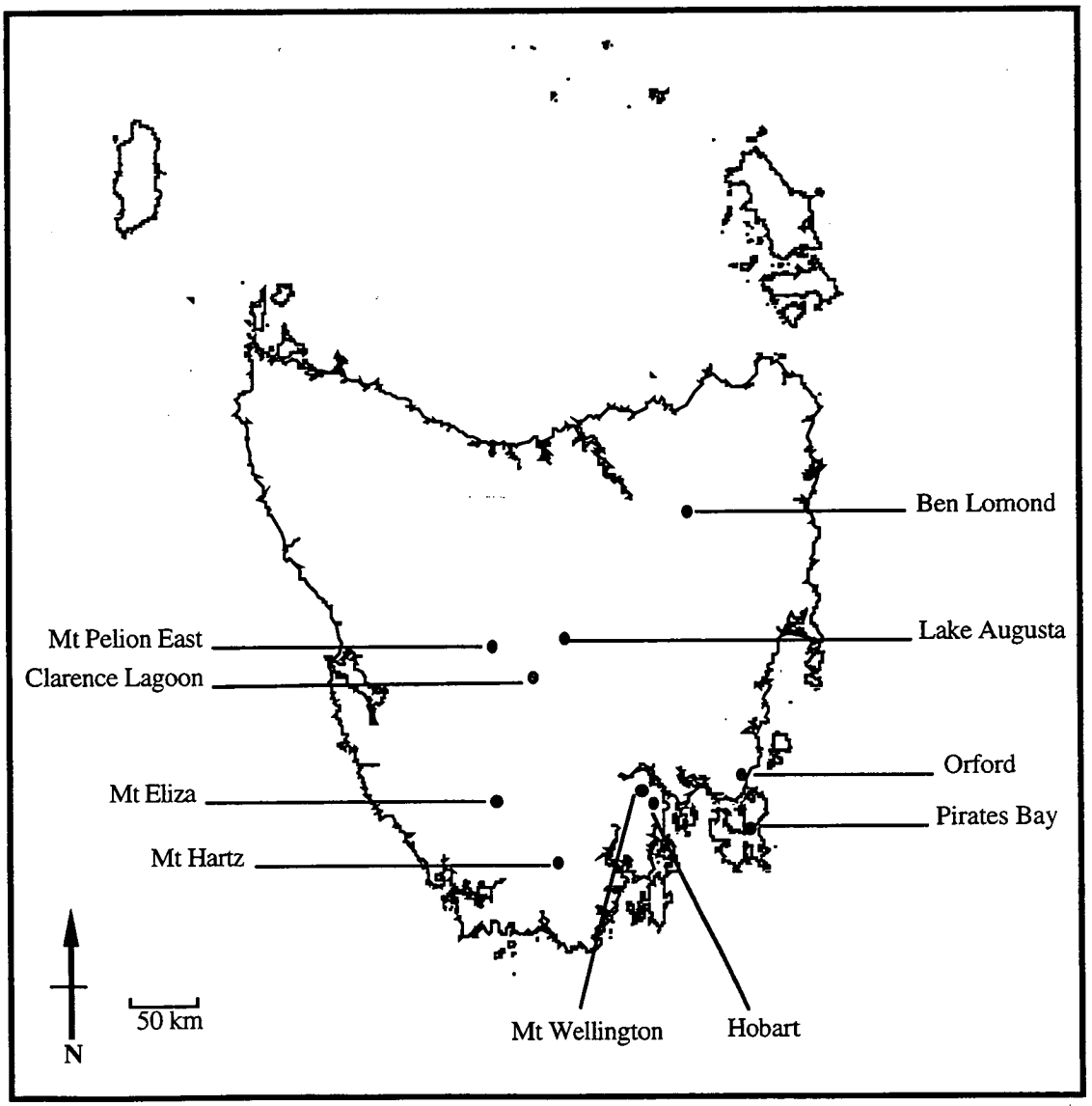


Figure 2.1 A map of Tasmania indicating the location of all the field sites. An exact location reference for each site is provided in the field descriptions.

The alpine vegetation of Tasmania is noteworthy for its many endemic species and unusual flora such as cushion plants (eg. *Abrotanella* spp. and *Donatia novae-zelandiae*), the deciduous beech (*Nothofagus gunnii*), and the pandani (*Richea pandanifolia*), the largest member of the Epacridaceae family in the world. There is a high degree of woody plants (Kirkpatrick *et al.*, 1995), including many alpine conifers. *Athrotaxis*, which includes King Billy pine (*A. selaginoides*) and pencil pine (*A. cupressoides*), is the only extant genus of the redwood family (Taxodiaceae) in the southern hemisphere.

There are three main habitat types found in alpine Tasmania: the alpine woodlands (Plate 2.2); the alpine heaths (Plate 2.1); and the dolerite boulder fields (Plate 2.3) (Collins, 1990). The alpine woodlands are typical of dolerite-capped mountains in Tasmania, although species composition depends upon the location. This community type occurs between 1000 and 1100 m. The canopy coverage in the woodlands is less than 30%, allowing light to penetrate to the ground in most areas. As a result, there is a vigorous understorey, up to about 1.5 m in height. The litter layers are composed mainly of eucalypt debris, up to 30 cm in depth. The canopy reaches a maximum of 10 m in height and is dominated by eucalypt species.

Alpine heaths are common above 1100 m. This vegetation will also occur at slightly lower altitudes in areas where waterlogging and acidic peat soils occur, causing edaphic disclimaxes in the vegetation (Bowman, 1986). The microhabitats found in these areas are described as heath in this thesis. There are no trees present and the vegetation height does not exceed 1.5 m. The ground cover is low and dense and there is a moderate level of species diversity. These areas are dominated by woody species but do not have any trees. Alpine heath is very extensive, incorporating many woody species, such as *Orites* spp., *Richea* spp. and *Ozothamnus* spp. Conifers are also common (eg. *Diselma archeri*, *Microcachrys tetragona* and *Podocarpus lawrencei*) and can attain dominance in coniferous heaths. Grasses (eg. *Poa* spp.), sedges (eg. *Carex*

spp., *Empodisma minus*) and pineapple grass (*Astelia alpina*) can each comprise a significant component of the flora, occasionally attaining dominance by themselves. The bolster heaths, consisting of cushion plant communities, in which the shrubs have become extremely low and dense as protection against the harsh environment, are found in the more exposed areas.

The third distinct type of microhabitat present in alpine Tasmania is represented by extensive areas of dolerite boulder fields (Plate 2.3). There is very little or no vegetation other than encrusting lichen and mosses on the surface of rocks. Boulders range in diameter from 0.5 to 8 m.

Plate 2.1 Mt Eliza, with Mt Anne in the background, showing alpine heath consisting of woody shrubs and cushion plants.

Plate 2.2 An alpine woodland located on Mt Wellington at approximately 1000 m a.s.l.; with a canopy dominated by eucalypts and a shrubby understorey.

Plate 2.3 A dolerite boulder field located on Mt Wellington. There is very little vegetation present and boulders range in size from 0.5 up to 8 m in diameter.

Ben Lomond

Ben Lomond is a small group of peaks located in the northeast of Tasmania. This region experiences a mild maritime climate with a comparatively small diurnal range of temperatures, although this maritime influence decreases with distance from the sea and altitude. Snow can be experienced at any time of the year, although late winter through spring is generally the period of heaviest falls. Hail storms are irregular, but most likely in spring. Frost is common throughout the year. Daily temperatures will not usually get above 25°C in summer or below 2°C in winter. However, extreme minima of -7°C are not uncommon overnight during winter.

The peaks of Ben Lomond are formed from Jurassic dolerite. They are flat-topped with gentle upper slopes and steep scarps. Field work was conducted on Legges Tor (147°40′E 41°32′S) which has an altitude of 1572 m. Rock outcrops and boulder fields are dominant above 1000 m. Small areas of stony soils and peat support heath vegetation. Below 1000 m eucalypt woodlands occur.

Niveoscincus greeni was the species studied at this site and was very common above 1100 m. *Niveoscincus ocellatus* was observed in the boulder fields up to about 1100 m and some overlap occurred with *N. greeni*. *Niveoscincus pretiosus* and *N. metallicus* were observed up to the tree-line. No other reptile species were caught during the study period.

Lake Augusta

Lake Augusta (146°31′E 41°52′S) is located on the Tasmanian Central Plateau at an altitude of approximately 1000 m. Sub-alpine woodlands would occur elsewhere at this altitude. However, this site experiences the lowest average temperatures in Tasmania and is subjected to heavy snow falls, hail storms and frost throughout the year. Temperatures of -2°C are common in winter and in summer temperatures rarely rise above 23°C.

The topography of the Central Plateau has been shaped by Pleistocene glaciations. The plateau was covered by a large ice-sheet and much of the area has been levelled by the abrasive force of the ice sheet. The area surrounding Lake Augusta is flat and windswept and the soils are waterlogged and acidic. As a consequence there are very few trees and the woody shrubs which dominate do not grow above 1.5 m. The result is a heathland very similar in structure and composition to that usually found at higher altitudes.

Narrow sandy shores, composed of coarse dolerite sand surround Lake Augusta. Large outcrops of dolerite boulders occur in irregular patches along these sandy shores. *Niveoscincus ocellatus* was studied at this site, where it is common within the boulder outcrops. *Niveoscincus metallicus* was also present in the heathland but not on the boulders. The only other reptile species caught at this site during the study was *Drysdalia coronoides* (white-lipped snake).

Mt Eliza

Mt Eliza (146°24′E 42°58′S) is located in the southwest of Tasmania, which is between the latitudes of 42° and 43°45′S in the 'Roaring Forties'. The southwest of Tasmania has a severe climate. The prevailing airstream is a moisture-laden westerly from the Southern Ocean. Rain, sleet, hail and snow are often brought in by gales and can be expected at any time of the year. Rapid changes in weather are typical for this region. Seaonal temperatures range from 9.6° to 19.8°C in summer and 3° to 8.8° in winter. However, these are only trends, as temperatures are very unpredictible and large variations occur in all seasons.

The dolerite peak of Mt Eliza and its nearby plateau (Plate 2.1) were modified by two large valley glaciers (Collins, 1990). Consequently, extensive areas of dolerite boulder fields occur on the western and eastern faces of Mt Eliza. To the northeast of the peak extends a large plateau which is dominated by heath. The Eliza Plateau is at an altitude

of 1200 m. Below the peak, at an altitude of 1000 m, is a band of woodland with a sparse eucalypt canopy.

Field work on *N. orocryptus* was conducted in all three habitat types found at Mt Eliza. *Niveoscincus microlepidotus* occurred in the boulder fields and heath, while *N. orocryptus* was found only in the woodland. There did not appear to be any overlap of the species. The only other reptile species seen at this site during the study was *Drysdalia coronoides* (white-lipped snake).

Mt Hartz

Mt Hartz (146°46′E 43°15′S) is located in south-western Tasmania, on the edge of the World Heritage Area. Mt Hartz, like Mt Eliza, is composed of Jurassic dolerite which has been shaped by Pleistocene glaciations. Many cirques, glacial moraines and lakes are found in the immediate vicinity of Mt Hartz. The field site extended from Lake Esperance at about 1000 m up to the peak at 1255 m. There was a gradation of habitat types from shrubby heath with stands of pencil pines (*A. cupressoides*) and the deciduous beech (*Notofagus gunnii*) surrounding the lake, to bolster heath on the Hartz Pass at approximately 1100m and final large fields of dolerite boulders on the slopes of Mt Hartz.

Niveoscincus orocryptus and *N. microlepidotus* were present at this field site and both species were studied. *Drysdalia coronoides* (white-lipped snake) was observed a number of times in the open heath close to the lake. No other reptile species were observed during the study period.

Mt Pelion East

Located in central Tasmania, just east of the Tasmania's highest peak, Mt Ossa, Mt Pelion East (146°04′E 41°50′S) rises to 1432 m. Much of this area was covered by Pleistocene glaciations that have carved the dolerite into the narrow pointed peak of

Mt Pelion East. Exposure to severe weather conditions has resulted in the development of large areas of bolster heath. Much of the upper slopes of the mountain is covered by cushion plants. The boulder fields are extensive and there are also large areas of scree slopes, composed of large flat rocks loosely piled. These appeared to have fallen from the vertical face of the peak.

Further down the slope the vegetation grades from bolster heath into shrubby heath and finally woodland on the Pelion Gap (the pass between Mt Pelion East and Mt Ossa). Field work was conducted on the upper slopes in the shrubby heath, bolster heath and the rocky outcrops. *Niveoscincus greeni* was studied here, where it was found in large numbers in the boulder fields and scree slopes. It was never collected in the heath or woodland. *Niveoscincus microlepidotus* was found in the areas of heath and did not overlap with *N. greeni.* No other reptile species were observed at this field site.

Mt Wellington

Mt Wellington (147°13′E 42°53′S) is located in southern Tasmania on the edge of the Derwent River Valley, forming a backdrop to the city of Hobart. The study site is located at an altitude of approximately 1080 m, on the eastern face of Mt Wellington below the Big Bend. This is a sub-alpine to alpine transition zone (Plates 2.2 & 2.3). Three distinct microhabitats were identified at the study site: (1) sub-alpine woodland; (2) alpine heath; and (3) boulder fields. These occur in a mosaic of small patches which have well defined boudaries.

There are high abundances of reptile fauna at this site but the species diversity is low. Apart from the species examined in this study at this site, which was *Niveoscincus microlepidotus*, the only other *Niveoscinus* species observed over the study period were *N. metallicus* and *N. pretiosus*. Throughout the study three other reptile species were observed: *Notechis ater* (tiger snake), *Drysdalia coronoides* (white-lipped snake) and a single specimen of *Cyclodomorphus casuarinae* (she-oak skink).

2.1.2 Forest Habitats

The forest communities in Tasmania include both schlerophyll and temperate rain forests. The relationship between these is complicated by the influence of soil fertility, aspect and fire (Jackson, 1981). Eucalypts are only absent in areas of low fire frequency (>200 years) and rain forest is replaced by sclerophyll forest as the fire frequency increases.

The most abundant structural forms in Tasmania are the open and tall open forests (Plate 2.4). These are mostly sclerophyllous and form the most common plant communities in central and eastern Tasmania. This vegetation type is found mainly on gradational and duplex soils which have formed on dolerite, granite, sandstones and Tertiary deposits. Open forests give way to tall open forests in areas of higher rainfall and elevation.

In the dry sclerophyll forests the shrub layer is low and sparse compared with the tall dense understorey found in the wet sclerophyll forests. The principal understorey species are *Acacia* spp., *Casuarina* spp., *Leptospermum scoparium*, *Melaleuca ericifolia*, *Epacris* spp. As the rainfall increases *Helichrysum* spp., *Bedfordia* spp., *Olearia* spp., *Pomaderris apetala* and *Zieria arborescens* become the dominant species. The dominant eucalypt species in these forests, forming the canopy, are *Eucalyptus obliqua*, *E. amygdalina*, *E. viminalis* and *E. ovata*. *Eucalyptus obliqua* is replaced by *E. delegatensis* in areas of higher rainfall and elevation. *Eucalyptus regnans* is common in sheltered situations on deep, well drained soils, while *E. globulus* is common in southern Tasmania. The distribution and dominance of these species depends upon the climate, soil and aspect.

Rainforest, mixed forest, and wet sclerophyll forests are common in western Tasmania (Plate 2.5). These forests occur in areas of high rainfall on Precambrian quartzite, phyllite, sandstone and schist in the more protected areas where greatest soil

accumulation is likely. Rainforest canopies are dominated by *Notofagus cunninghamii*, *Atherosperma moschatum*, *Eucryphia lucida*, *Phyllocladus aspleniifolius* and occasionally *Acacia melanoxylon*. Understorey species commonly include *Dicksonia antarctica*, *Anopterus glandulosus*, *Blechnum wattsii*, and *Orites diversifolia*. Moss covers fallen branches and trunks. Lichens, bryophytes and epiphytic ferns are also widespread.

Mixed forests have a eucalypt conopy over a tall understorey of common rainforest species. Mixed forest and wet sclerophyll forests are found in areas which could support rainforest with an absence of fire. Some of the tallest eucalypts in Australia occur in these forests; heights of over 75 m are common, while some trees exceed 90 m. These trees are usually *Eucalyptus regnans* or *E. obliqua*. However, *E. nitida* is the most common eucalypt in western Tasmania. It can vary in height from 5 m in scrub forest on dry, shallow soils to 40 m on better soils. The understorey in the wet sclerophyll forests commonly consists of the musk (*Olearia argophylla*), blanket leaf (*Bedfordia salicina*) and many wattles (*Acacia* spp.).

Clarence Lagoon

Clarence Lagoon (146°19′E 42°04′S) is on the southern side of central Tasmania, on the edge of the Central Plateau World Heritage Area. It is a small glacial lake at about 1000 m a.s.l., formed behind the remnants of a glacial moraine. Consequently, the southern shore of the lake is surrounded by a narrow band of boulders. The weather at this site is unpredictable and variable; during this study snow was found at the site on a number of occasions during spring and summer. The annual rainfall is high and seasonal temperatures range from 9.6° to 22.3°C in summer and 3° to 11.8° in winter. The soil surrounding the lake is shallow and dolerite boulders break through in many areas. This site becomes more sheltered as the land drops down steeply to below the remnant moraine; the temperature is often 4°C warmer here than at the lake edge. The soil here is a deeper duplex soils formed from dolerite.

The vegetation close to the lake edge is open sub-alpine forest (Plate 2.4). The canopy is low and sparse allowing extensive light to reach the ground. However, the understorey is patchy in most areas. Species common in sub-alpine areas are dominant, including *Richea* spp., *Epacris* spp., *Telopea truncata*, *Boronia citriodora* and *Bauera ruboides*. The vegetation away from the lake, which is more sheltered down the slope of the moraine, is very different and consists of tall mixed forest with a closed canopy in the very sheltered areas (Plate 2.5) and an open sclerophyll forest in the more exposed areas. There is a tall understorey of rainforest species in the sheltered areas and in the more exposed areas the understorey is composed of thick sub-alpine shrubs. There are clearings where it is too rocky to support an understorey; here the rocks are covered by a thick layer of moss and lichen. There are also many fallen trees creating breaks in the canopy.

Niveoscincus metallicus and *N. pretiosus* were studied at this field site, where there was a moderate diversity of reptile species with high abundances. *Niveoscincus metallicus* was found throughout the study area, while *N. pretiosus* was restricted to the tall forest. *Niveoscincus ocellatus* commonly basked on the boulders surrounding the lake. *Drysdalia coronoides* (white-lipped snake) was also observed a number of times close to the lake. The larger tiger snake (*Notechis ater*) was very common around the lake and on sunny days it was common to see up to ten snakes basking on rocks along the 500 m stretch of this study site which was adjacent to the lake.

Hobart

The Hobart field site was located in the University Reserve behind the University of Tasmania (147°20′E 42°55′S), on the base of the eastern slope of Mt Nelson. The area is disturbed by the recreational activities of the occupants of the surrounding suburbs and is frequently burnt. A fire burnt a large area close to the field site in the first year of this study. The soil is a dolerite based duplex typical of eastern and southern Tasmania.

The field site has two vegetation types: dry sclerophyll forest and grassland. The forest is typical of the Hobart area and consists of an open canopy of species such as *Eucalyptus obliqua*, *E. amygdalina*, *E. viminalis* and *E. ovata*. The understorey is sparse and shrubby. The ground is rocky with thick litter layers of bark and fallen leaves around the bases of the eucalpyts. The grassland is an area which has been cleared and exotic grass and weed species are dominant.

Pseudemoia entrecasteauxii was studied here, where it was found in the grassland and the edge of the forest. *Niveoscincus metallicus* was also found throughout this study site. No other reptiles were observed at this site during the study.

Plate 2.4 Tall dry sclerophyll forest located on the banks of Clarence Lagoon, with a eucalypt canopy and a sparse shrubby understorey.

Plate 2.5 Mixed forest located in the sheltered areas surrounding Clarence Lagoon. The canopy is dominated by eucalypts and the understorey consist of rainforest species, such as *Nothofagus cunninghamii*.

Orford

This field site is located approximately 2 km inland from the small township of Orford (147°51′E 42°34′S). The climate is mild, although it has a high fire frequency, and extensive areas surrounding Orford were burnt during the first year of this study. The field site is warm and dry, with temperatures often above 25°C during summer. The topography is dominated by low hills of weathered dolerite, which support a shallow soil with numerous rocky outcrops.

The vegetation is dry sclerophyll forest with an open canopy and sparse understorey. In the damp gullies the forest changes to wet sclerophyll with a tall dense understorey. The field site was located in an area of dry sclophyll forest which had many small rocky outcrops. This type of habitat is dominant along the entire east coast of Tasmania.

This field site had the highest diversity of reptiles observed during this study. The two species studied here were *N. metallicus* and *N. ocellatus*. *Niveoscincus pretiosus* occurred in the wet sclerophyll areas; a number of *Psuedemoia entrecasteauxii* were caught during this study. Groups of *Egernia whitii* inhabited large burrow systems on sunny slopes and several *Cyclodomorphus casuarinae* were seen. The eastern mountain dragon (*Tympanocryptis diemensis*), the only lizard species occurring in Tasmania which is not a skink, was commonly seen basking on hot days. Both *Notechis ater* (tiger snake) and *Drysdalia coronoides* (white-lipped snake) were observed during this study.

Pirates Bay

Pirates Bay (147°56'E 43°01'S) is located on the Tasman Penninsula in south eastern Tasmania. The field site is beside the beach at the northern end of the bay. Steep cliffs of sandstone and dolerite delineate the boundary between beach and forest. The Bay is surrounded by a ring of small mountains. The climate is mild but unpredictable. Large storms come in off the ocean bringing high winds and heavy rain throughout the year. Mist and low cloud often sit on the mountains for days, shadowing the field site.

The high rainfall in this area has resulted in tall forests dominated by wet sclerophyll species. The dominant eucalypt species is *E. regnans*, which towers over a dense understorey of species such as *Olearia* spp., *Exocarpus* spp., *Leptospermum* spp. and *Bedfordia* spp. The tall canopy and thick understorey let little light reach the ground. Fallen trees provide breaks in the canopy and basking sites for lizards.

Niveoscincus pretiosus was the species studied at this site. The only other lizard species seen was *N. metallicus*, which was common around disturbed areas, especially houses and roads. A number of tiger snakes (*Notechis ater*) were observed during the study period.

Mt St Leonards

This site (145°32'E 37°33'S) forms part of the Main Divide in southeastern Victoria. The rainfall is high, exceeding 900 mm per year. The eucalypt forests are commonly tall (above 30 m), and usually have a dense understorey of tall shrubs or small trees, especially in sheltered valleys.

The dominant canopy species is the Mountain Ash (*Eucalyptus regnans*). This species occurs south of the Divide at altitudes of 500-1000 m and often exceeds 60 m in height, with understorey trees (especially wattles) reaching a third of this height. Although the mountain forests appear dense, the canopy of tall eucalypts is relatively open, allowing a moderate amount of light through to the understorey. Tree ferns, daisy bushes (*Ozothamnus* spp.) and *Pittosporum* spp are common understorey species.

Niveoscincus coventryi was studied at this site. The other two reptile species which were commonly observed were the water skink (*Eulamprus tympanum*), which basked on fallen tree trunks, and *Psuedemoia spenceri*, an arboreal skink which lives in large numbers on dead tree trunks which are still standing vertically.

2.2 Identification of species

The genus *Niveoscincus* comprises a group of small to medium sized lygosomine skinks, diagnosed by well-developed prefrontal shields, paired or fused frontoparietals, a distinct interparietal shield and a moveable lower eyelid with a moderate to large transparent palpebral disc (Hutchinson *et al.*, 1989). These lizards have well-developed pentadactyl limbs.

The colour of this genus ranges from brown through to green flecks. The patterning and colour of the head, body and tail vary depending on the species. *Niveoscincus greeni*, for example has a dark dorsal surface with green flecks, while *N. microlepidotus* has dorsal scales which are flecked and edged with black, forming a crude checker-board

pattern (Plate 2.6). *Niveoscincus ocellatus* is the most recognisable species, with a light brown dorsal surface which is covered by distinct black flecks (Plate 2.7). In a number of the species a dorsolateral scale row is flecked producing a light dorsolateral stripe. *Niveoscincus pretiosus* has very distinct dorsolateral stripes (Plate 2.8), while *N. ocellatus* lacks these. The ventral surface is unmarked and ranges in colour from medium to light grey to light olive. Many individuals of *N. metallicus* and less commonly *N. pretiosus* have a red or pink tinge to their ventral surface. The cause of this is unknown, but males are more strongly coloured than females (Swain and Jones, 1994).

The identification of some species of *Niveoscincus* is difficult. The colour and patterning in some species, such as *N. metallicus,* is highly variable and identification by scale counts is necessary (Cogger, 1992). Even scale counts will not consistently distinguish between *N. orocryptus* and *N. microlepidotus,* which are very similar morphologically and exhibit overlap in the range of paravertebral scale numbers (often used in identification).

Identification was carried out using a key developed by Swain (pers. comm.).

Plate 2.6 Adult male *Niveoscincus microlepidotus* (svl 62 mm) from Mt Wellington.

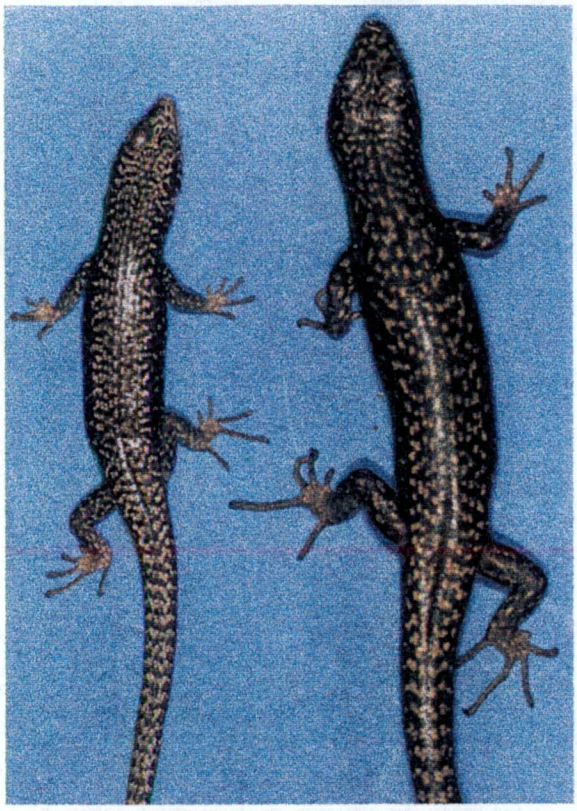


Plate 2.7 Two adult male *Niveoscincus ocellatus*; the individual on the left is from Orford (svl 53 mm), while the one on the right is from Lake Augusta (svl 71 mm).

Plate 2.8 An adult male *Niveoscincus pretiosus* (svl 48 mm) from Clarence Lagoon.

2.3 Capture and housing of lizards

Lizards were captured using a noose gun or by hand. Neither of these methods appeared to damage animals. Previously (Melville, 1994), some success had been gained by luring lizards from inaccessible positions with a baited line (live meal worm attached to a line by cotton thread). This method proved unsuccessful in this study as it was very difficult to locate lizards in the dense undergrowth or the boulder fields. At some of the field sites loose rocks could be turned to capture inactive lizards.

Following the capture of a lizard its snout-vent length (SVL) and sex were determined. Animals required for laboratory work were transported back to the university in plastic bags stored in a cool, shaded location. All subjects were then toe-clipped and tagged with a visual identifier. None of the rearleg toes or large frontleg toes were clipped, to avoid problems with performance trials. Adhesive cloth tape was used to tag subjects and an identifying number was assigned to each individual. Tags were shed during moulting and had to be regularly replaced.

Lizards were kept in the Reptile House at the University of Tasmania. The room in which the lizards were housed was lit by fluorescent tubes for 14 hours per day at an intensity of 20000 lux. The temperature was set at approximately 14°C. Light globes inside tin cans suspended over each cage served as basking sources and provided a temperature gradient of 14 - 35°C within each cage. The basking lights were controlled to provide ten hours of basking light each day. Lizards were housed in plastic lunch containers (20 x 30 x 10 cm) with netting secured over the top (Plate 2.9). No more than five individuals were kept in each container. Some lizards (especially males of the alpine species) had to be housed on their own as they tended to fight and injure other lizards. Absorbent gravel was provided as a substrate, small clay tiles were provided for basking, and plastic squares for shelter. Lizards were fed twice weekly on meal worms, tinned cat food and mashed banana.

2.4 Permits

The research described here was carried out under Ethics Permit 95048 issued by the University of Tasmania. Field work in Tasmanian national parks was carried out under collecting permits issued by the Department of the Environment and Land Management (Permit FA 95146). Collecting and obersvation of lizards on Mt Wellington was contucted using a permit issued by the Hobart City Council (Permit JH 70-1-5). All field work undertaken in Victoria was covered by a permit from the Department of Conservation and Natural Resources (Permit RP-95-129).

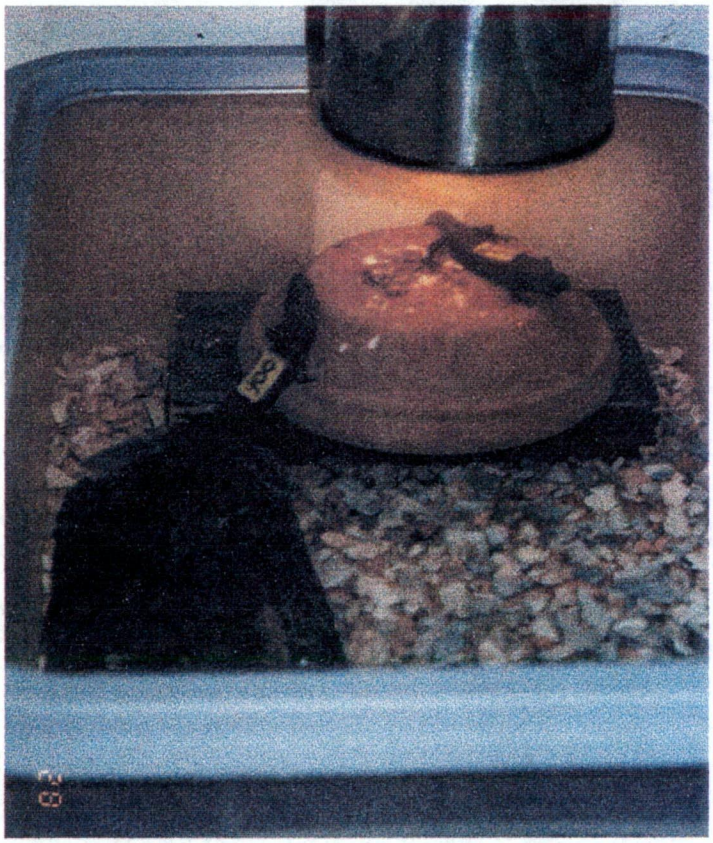


Plate 2.9 Lizards were housed in plastic containers and provided with a heat source and shelter.

CHAPTER THREE

Phylogenetic Relationships within *Niveoscincus*

3.1 Introduction

3.1.1 Pertinence of phylogeny to ecological morphology

The comparative method in evolutionary biology can be used to draw evolutionary inferences through interspecific comparisons (eg. Felsenstein, 1985; Brooks and McLennan, 1991; Harvey and Pagel, 1991; Lynch, 1991; Martins and Garland, 1991; Losos and Miles, 1994). Many studies assume that the patterns revealed in an ecomorphological analysis reflect adaptation to prevailing selective pressures (Losos and Miles, 1994). However, such interpretations are problematic in the absence of historical information, because phylogenetic effects will confound conventional statistical methods when examining adaptation (Brooks and McLennan, 1991). For example, the presence of a given character in more than one species in a clade may be attributable to either shared ancestry or independent evolution of the trait (Losos and Miles, 1994). Taxa which share a trait due to a common ancestry cannot be viewed as independent points for statistical analysis. Furthermore, in the absence of historical information, evolutionary rate and direction cannot be deduced (Felsenstein, 1985).

Inclusion of phylogenetic information (topology and branch lengths) in a comparative study will allow more accurate insight into patterns seen in living organisms (Garland *et al.*, 1993). Consequently, it was essential to have a reliable phylogeny to allow a valid comparative analysis of the evolution of locomotion, behaviour, ecology and morphology in the genus *Niveoscincus*.

3.1.2 Phylogenetic relationships in *Niveoscincus*

Current evidence suggests that the genus *Niveoscincus* has diverged recently, within the last 5 million years, as fewer than 10 albumin ID units separate the Tasmanian endemic species (Hutchinson *et al.*, 1990). Hutchinson and Schwaner (1991) found

fixed allelic differences between the species but *N. orocryptus* and *N. microlepidotus* were not distinguishable electrophoretically at some locations. They suggested that a single species may have given rise to four modern lineages during the Pleistocene glaciations: *N. ocellatus, N. pretiosus, N. metallicus*, and a group consisting *of N. palfreymani, N. greeni, N. orocryptus* and *N. microlepidotus*. However, allozyme electrophoresis was unable to confidently establish the phylogenetic relationships between *N. ocellatus, N. pretiosus* and *N. metallicus* (Figure 3.1).

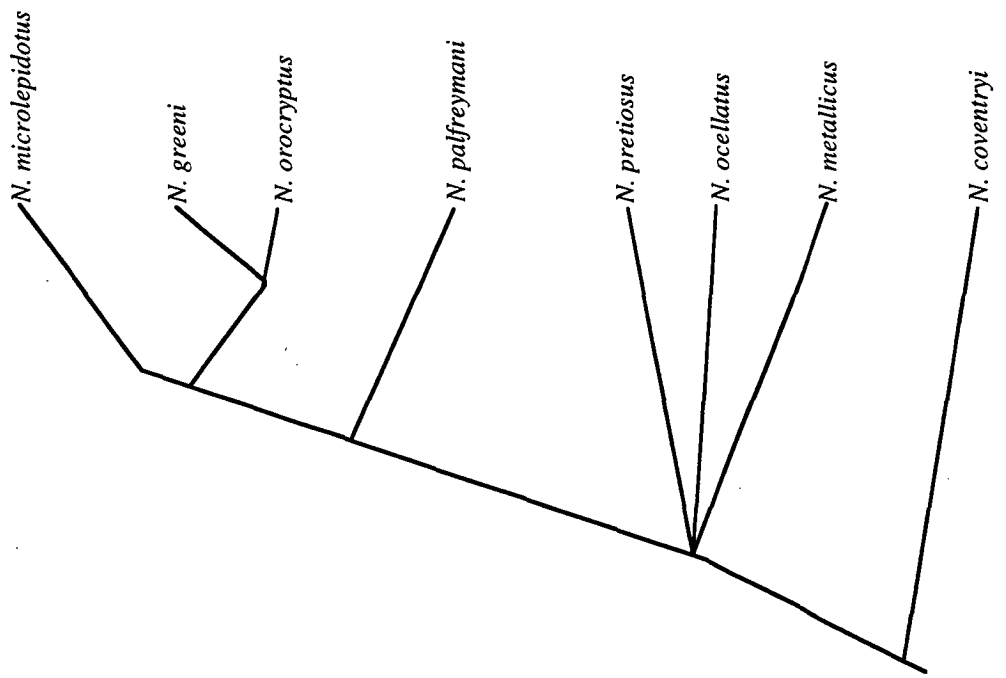


Figure 3.1 Diagramatic representation of consensus tree from allozyme electrophoretic work on *Niveoscincus*, showing the unresolved relationships between *N. metallicus, N. ocellatus* and *N. pretiosus* (Hutchinson and Schwaner, 1991).

Allozyme electrophoresis is a powerful tool for providing data concerning gene flow between populations (Richardson *et al.*, 1986). However, use of electrophoretic distance data in phylogenetic studies is more controversial (Hutchinson and Schwaner, 1991). Recently diverged taxa will not suffer from the confounding effects of homoplasy of electromorphs and the non-additivity of distance values may not be a major problem (Richardson *et al.*, 1986). Hutchinson and Schwaner (1991) suggested that allozyme electrophoresis was unable to fully resolve the phylogenetic relationships of *Niveoscincus* because the genetic divergence between the major

lineages is sufficiently large that homoplasy in allele mobility is likely to have had some effect. Consequently, a phylogenetic analysis based on DNA-sequence variation of the mitochondrial gene cytochrome *b* was undertaken in this study to clarify phylogenetic relationships within *Niveoscincus*.

This is currently the only research which has investigated phylogenetic relationships in *Niveoscincus* using DNA sequencing techniques. It will allow the examination of the molecular phylogeny of *Niveoscincus* and possible vicariant biogeographic speciation, thus addressing the possible role of Pleistocene glacial events in speciation and in shaping the current distributions of the *Niveoscincus* species. The results from this analysis will be used as the basis for the comparative phylogenetic analyses in Chapter 8.

3.1.3 Mitochondrial genes

Mitochondrial DNA (mtDNA) has been widely used in phylogenetic studies because it evolves rapidly and provides an abundance of genotypic characters. However, there have recently been some doubts expressed concerning its reliability for predicting phylogenies (Hoelzer, 1997). A phylogenetic inference based on DNA-sequence variation can be incorrect even though the gene tree has been correctly resolved (Wu, 1991; Doyle, 1992). The mtDNA tree may not be congruent with the species tree in situations where an ancestral species is polymorphic for the gene and sorting of lineages is derived from the alternate haplotypes (Moore, 1995). The reliability of mtDNA is limited by lineage sorting, because the mitochondrial genes are inherited as a single linkage group and do not provide independent estimates of the species tree. However, Moore (1995) concluded that a mitochondrial gene tree is more likely to be congruent with the species tree than is a nuclear gene tree.

The probability that a gene tree will track a species tree depends on the effective population size of ancestral species; the smaller the effective population size, the higher the probability that a given tree will track the species tree (Moore, 1995). The

population genetics of the mitochondrial genome are determined by an effective population size that is one fourth as large as that of a nuclear-autosomal gene, because the mitochondrial genome is haploid and maternally inherited.

Hoelzer (1997) suggests that, in situations where clades exhibit female philopatry and male dispersal, or a polygynous mating system, mtDNA-gene trees may be less reliable indicators of a species phylogeny than a nuclear-gene tree. Moore (1997) agrees that both polygyny and female philopatry reduce the effective population size of nuclear genes relative to that of the mt-genome. Thus, under these circumstances a nuclear tree may provide a better inference of the species tree than the mt-haplotype tree. Moore (1995) provided a theoretical basis for preferring mt-DNA gene trees over nuclear-gene trees when estimating species phylogenies. This argument is based on a number of assumptions. Among these are that nucleotide substitutions are neutral, the species population is panmictic and progeny are procreated by equal numbers of males and females; that is, variation in reproductive success is the same for both males and females (Moore, 1997).

Sampling multiple unlinked genes would increase the probability of correctly inferring a species tree. However, because the mitochondrial genes are inherited as a single linkage group they provide only one independent estimate of a species tree. The only alternative is to resolve phylogenies for several unlinked nuclear-DNA sequences. However, it appears that a large number of nuclear-gene trees are required to improve upon the confidence based on the mitochondrial tree alone (Moore, 1995).

The mitochondrial gene cytochrome *b* is a popular tool for phylogenetic studies and has been used to investigate a wide range of divergence times (Graybeal, 1994). Mitochondrial protein coding genes generally evolve too rapidly to provide reliable information on ancient divergences (Hillis and Huelsenbeck, 1992). Most studies indicate that cytochrome *b* is best suited for the more recent Cenozoic (<65 mya) divergences (Harrison, 1989). However, there is increasing evidence that rates of

sequence evolution vary between taxa (Martin and Palumbi, 1993). Graybeal (1993) suggested that in bufonid frogs the cytochrome *b* gene is strongly constrained by selective forces, more so than in other vertebrates. Caccone *et al.* (1997) investigated the rate of sequence divergence in the cytochrome *b* gene of european newts (genus *Euproctus*). They found that cytochrome *b* rates were 3-7 times lower in salamanders than in other ectotherms. The variation in rates among vertebrates has been attributed to a series of physiological and life-history variables, including differences in body size and temperature (Caccone *et al.*, 1997).

3.2 Materials and Methods

A 307-bp region of the cytochrome *b* gene was sequenced for the eight species of *Niveoscincus* and one species of the sister taxon *Pseudemoia*. The analysis utilised at least two individuals of each species; for *N. orocryptus* and *N. microlepidotus* three individuals from each site were sequenced because of confusion about hybridisation between these species at Hartz Mountain and because there is some question whether *N. orocryptus* from Hartz Mountain and Mt Eliza are the same species (Hutchinson and Schwaner, 1991). The lizards sampled are listed below, along with abreviations used in this chapter to distinguish individual sequences and the field site from where samples were obtained.

1. *P. entrecasteauxii* (h) -Hobart
2. *P. entrecasteauxii* (o) - Orford
3. *N. palfreymani* (1) - Pedra Branca
4. *N. palfreymani* (2) - Pedra Branca
5. *N. coventryi* (1) - Mt St Leonards
6. *N. coventryi* (2) - Mt St Leonards
7. *N. pretiosus* (cl) - Clarence Lagoon
8. *N. pretiosus* (p1) - Pirates Bay

9. *N. pretiosus* (p2) - Pirates Bay
10. *N. orocryptus* (e1) - Mt Eliza
11. *N. orocryptus* (e2) - Mt Eliza
12. *N. orocryptus* (e3) - Mt Eliza
13. *N. metallicus* (o) - Orford
14. *N. metallicus* (bl) - Ben Lomond
15. *N. metallicus* (cl) - Clarence Lagoon
16. *N. microlepidotus* (e) - Mt Eliza
17. *N. microlepidotus* (1) - Mt Hartz
18. *N. microlepidotus* (2) - Mt Hartz
19. *N. microlepidotus* (m) - Mt Wellington
20. *N. orocryptus* (h1) - Mt Hartz
21. *N. orocryptus* (h2) - Mt Hartz
22. *N. orocryptus* (h3) - Mt Hartz
23. *N. greeni* (mr) - Mt Rufus
24. *N. greeni* (bl) - Ben Lomond
25. *N. greeni* (pe) - Mt Pelion East
26. *N. ocellatus* (cp) - Central Plateau
27. *N. ocellatus* (0) - Orford

The total DNA was extracted using the chelex technique (Walsh *et al.*, 1991). Synthetic oligonucleotide primers were used to amplify partial sequences of the mitochondrial gene cytochrome *b*. A 307-bp portion of this gene was amplified using the primers H15149 (5'CCCTCAGAATGATATTTGTCCTCA3') and L14841 (5'CCATCCAACATCTCAGCATGATGAAA3') (Meyer *et al.*, 1990). Reactions contained 1.5 mM $MgCl_2$. Double-stranded amplifications involved 40 cycles of denaturation at 94 °C (30 seconds), annealing at 45-55 °C (1 min) and extension at 72 °C. Purified PCR reactions were sequenced on an ABI Prism 377 autosequencer (Perkin-Elmer); sequencing reactions were run for both primers for each sample.

Sequences were aligned using the program Sequence Navigator. No insertions/deletions were identified, making alignment unambiguous. Percent divergences were calculated and phylogenetic analyses performed using PAUP version 3.1 (Swofford, 1993). Parsimony analyses were performed using the "branch and bound" search option, which guarantees to find the most parsimonious tree(s). Parsimony is a robust analysis, even under circumstances in which a large portion of a sequence is phylogenetic noise (Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992).

Confidence in the most parsimonious tree topology was assessed with the bootstrapping option, using heuristic searches on 1000 replicate data sets. Felsenstein (1985) proposed using the statistical test of bootstrapping to estimate confidence limits of internal branches in phylogenetic analyses. Bootstrapping has since become a common method for assessing confidence phylogenetic analyses (Hillis and Bull, 1993). Under conditions of equal rates of change, symmetric phylogenies, and internodal change of ≤20% of the characters, bootstrap proportions of ≥70% usually correspond to a probability of ≥95% that the corresponding clade is real (Hillis and Bull, 1993). Thus, in this analysis bootstrap values ≥70% were considered to indicate a high degree of confidence in the branching.

Differential weighting of codon positions was performed using the "set character weights" option. Base substitution is often separated into two categories, transitions (TIs) and transversions (TVs), for phylogenetic analysis of DNA sequences (Knight and Mindell, 1993). The recognition of the implications of TI bias by Brown *et al.* (1982) led to the widespread practice of increasing the weight of TVs over TIs for phylogenetic analysis. When sequences representing divergences several million years old are compared, TIs make up roughly 90% of the changes and TVs 10% (Brown *et al.*, 1982). However, the percentage of TIs steadily declines as the time of divergence between the taxa increases, until, for divergences ≥20 million years old, TIs have fallen to near 50% (Knight and Mindell, 1993). Transitions then remain near this level for more ancient divergences, dating to several hundred million years old. This is an

indication of saturation by multiple changes. Therefore, it is not an indicator of phylogeny but is largely "noise" (Hillis and Huelsenbeck, 1992; Knight and Mindell, 1993). When all character states in this analysis were taken into account, divergences among taxa were fairly high (Table 3.1); this is especially true for third-codon positions. Given the tendency for mitochondrial sequences to show saturation effects after divergences of 15-20% (Brown *et al.*, 1979), saturation is likely to be a problem for these data, especially for third codon positions. Hence, I chose to weight the characters (TV:TI ratio 4:1). The neighbour-joining method (Saitou and Nei, 1987) in PHYLIP was used to construct phylogenetic trees from distance matrices.

3.3 Results

3.3.1 Sequence data

Cytochrome *b* sequence variation between samples was observed at a total of 100 nucleotide positions (Figure 3.2). The majority of nucleotide base substitutions were observed at third codon positions, with fewer at first and second codon positions. At both first and third codon positions transition substitutions predominated over transversion substitutions, while at second codon positions only three transitions and no transversions were observed (Figure 3.2).

Base substitutions at first and second codon positions were responsible for twelve and two amino acid replacements respectively. Single amino acid replacements were a result of nucleotide base substitutions at third codon positions. No distinct patterns were evident in amino acid replacements, although the residue of leucine was frequently involved. Seven base substitutions observed at the first codon positions were conservative, not resulting in amino acid replacement as leucine remained encoded.

Table 3.1 Percentage sequence divergences (below diagonal) and observed number of substitutions (above diagonal) for each pair-wise comparison of taxa.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1. *P. entrecasteauxii* (h)	-	7.5	16.0	16.0	19.2	19.2	13.7	14.3	14.3	14.7	17.9	16.6	21.2	15.3	23.8	19.2	18.9	19.2	16.3	17.6	16.6	18.9	16.3	17.9	15.6	16.9	18.2
2. *P. entrecasteauxii* (o)	23	-	20.2	20.5	20.8	20.8	18.2	18.9	18.9	17.9	21.5	20.5	24.4	20.8	26.1	23.1	22.8	22.1	21.8	20.8	22.1	21.8	21.8	21.8	21.8	22.5	18.9
3. *N. palfreymani* (1)	49	62	-	0	7.8	7.8	8.8	8.8	9.4	8.5	7.2	10.4	17.3	12.1	21.2	13.4	11.7	13.4	10.1	11.1	10.4	13.0	13.7	15.0	14.0	13.7	15.0
4. *N. palfreymani* (2)	49	63	0	-	7.8	7.8	8.8	8.8	9.4	8.5	7.2	10.4	17.3	12.1	21.2	13.7	12.1	13.7	10.1	11.4	10.4	13.4	13.7	15.0	14.0	13.7	15.0
5. *N. coventryi* (1)	59	64	24	24	-	0	11.7	12.1	11.7	9.1	8.8	12.1	20.2	15.3	23.1	15.0	15.0	15.3	12.4	13.0	12.7	15.0	16.6	16.9	16.6	16.6	14.7
6. *N. coventryi* (2)	59	64	24	24	0	-	11.7	12.1	11.7	9.1	8.8	12.1	20.2	15.3	23.1	15.0	15.0	15.3	12.4	13.0	12.7	15.0	16.6	16.9	16.6	16.6	14.7
7. *N. pretiosus* (cl)	42	56	27	27	36	36	-	1.3	1.3	6.8	7.2	7.8	17.3	11.7	19.9	14.0	11.7	13.7	10.4	11.7	10.7	13.4	9.8	11.4	10.1	10.4	13.7
8. *N. pretiosus* (p1)	44	58	27	27	37	37	4	-	0.7	7.2	7.5	8.1	17.6	12.4	20.2	14.3	12.1	14.0	10.7	12.1	11.1	13.7	10.1	11.7	10.4	11.1	14.0
9. *N. pretiosus* (p2)	44	58	29	29	36	36	4	2	-	6.8	7.2	7.8	16.9	11.7	19.5	14.0	11.7	13.7	11.1	12.4	11.4	13.4	10.4	12.1	10.7	11.1	14.3
10. *N. orocryptus* (e1)	45	55	26	26	28	28	21	22	21	-	2.9	3.6	17.3	14.3	17.9	10.7	12.7	10.7	11.7	12.1	12.1	10.4	13.0	12.7	12.4	13.7	12.1
11. *N. orocryptus* (e2)	55	66	22	22	27	27	22	23	22	9	-	5.5	19.2	14.3	23.1	14.0	13.7	13.7	12.7	13.7	13.0	13.4	15.0	15.3	14.3	14.7	15.6
12. *N. orocryptus* (e3)	51	63	32	32	37	37	24	25	24	11	17	-	18.9	15.3	21.5	10.4	12.4	10.1	14.0	14.7	14.3	9.8	15.3	16.3	14.7	15.3	15.3
13. *N. metallicus* (o)	65	75	53	53	62	62	53	54	52	53	59	58	-	9.8	12.1	19.2	16.0	19.9	18.6	19.5	18.9	19.5	19.9	20.5	19.5	19.2	16.0
14. *N. metallicus* (bl)	47	64	37	37	47	47	36	38	36	44	44	47	30	-	14.7	14.7	13.0	15.0	12.7	14.0	13.0	14.7	14.3	16.0	14.0	13.0	14.0
15. *N. metallicus* (cl)	73	80	65	65	71	71	61	62	60	55	71	66	37	45	-	21.2	19.9	22.8	20.5	21.5	20.8	22.5	21.8	22.1	21.8	21.8	17.3
16 *N. microlepidotus* (e)	59	71	41	42	46	46	43	44	43	33	43	32	59	45	65	-	8.5	2.9	15.3	15.6	15.6	3.3	15.6	16.0	15.3	16.3	15.0
17.*N. microlepidotus* (1)	58	70	36	37	46	46	36	37	36	39	42	38	49	40	61	26	-	8.8	12.1	12.7	12.4	9.1	13.4	14.0	14.0	14.3	15.3
18.*N. microlepidotus* (m)	59	68	41	42	47	47	42	43	42	33	42	31	61	46	70	9	27	-	15.6	15.6	16.0	0.3	16.6	16.9	16.3	16.9	15.3
19. *N. orocryptus* (h1)	50	67	31	31	38	38	32	33	34	36	39	43	57	39	63	47	37	48	-	2.3	0.3	15.3	9.8	11.4	10.1	10.4	12.4
20. *N. orocryptus* (h2)	54	64	34	35	40	40	36	37	38	37	42	45	60	43	66	48	39	48	7	-	2.0	15.3	11.7	13.0	12.1	12.1	12.7
21. *N. orocryptus* (h3)	51	68	32	32	39	39	33	34	35	37	40	44	58	40	64	48	38	49	1	6	-	15.6	10.1	11.4	10.4	10.7	12.7
22.*N. microlepidotus* (2)	58	67	40	41	46	46	41	42	41	32	41	30	60	45	69	10	28	1	47	47	48	-	16.3	16.6	16.0	16.6	15.3
23. *N. greeni* (mr)	50	67	42	42	51	51	30	31	32	40	46	47	61	44	67	48	41	51	30	36	31	50	-	3.6	2.9	6.8	12.1
24. *N. greeni* (bl)	55	67	46	46	52	52	35	36	37	39	47	50	63	49	68	49	43	52	35	40	35	51	11	-	4.9	9.1	12.4
25. *N. greeni* (pe)	48	67	43	43	51	51	31	32	33	38	44	45	60	43	67	47	43	50	31	37	32	49	9	15	-	7.8	12.1
26. *N. ocellatus* (cp)	52	69	42	42	51	51	32	34	34	42	45	47	59	40	67	50	44	52	32	37	33	51	21	28	24	-	9.1
27. *N. ocellatus* (0)	56	58	46	46	45	45	42	43	44	37	48	47	49	43	53	46	47	47	38	39	39	47	37	38	37	28	-

3.3.2 Intraspecific variation in *Niveoscincus*

Cytochrome *b* sequences were obtained from more than one individual of most taxa. Identical sequences were obtained from the two samples of *Niveoscincus palfreymani* (Table 3.1) from Pedra Branca. This is the only location where this species occurs. Similarly, no divergence was detected between the two *N. coventryi* sequences from Mt St Leonards. There was also very little intraspecific variation between the sequences of *N. pretiosus*. However, considerable genetic variation was detected between the populations of *N. orocryptus, N. metallicus, N. microlepidotus, N. greeni* and *N. ocellatus*.

Niveoscincus orocryptus populations

Six cytochrome *b* sequences from two populations (Mt Eliza and Mt Hartz) of *N. orocryptus* were analysed (Table 3.1). Pairwise sequence divergence ranged from 0.3% (1 substitution) between two sequences from Mt Hartz to 14.7% (45 substitutions) between a Mt Eliza and a Mt Hartz sequence. The Mt Eliza genotype differed from that of Mt Hartz by a mean of 13.1%. The topology of the neighbour-joining and parsimony trees (Figures 3.4 & 3.5) both separated Mt Eliza and Mt Hartz populations. In each of these trees the Mt Hartz population is grouped with *N. greeni* and *N. ocellatus* to form one clade, while the Mt Eliza population is grouped with *N. pretiosus* to form a second clade.

Niveoscincus metallicus populations

A high level of intraspecific diversity was detected between *N. metallicus* populations. Pairwise sequence divergences ranged from 9.8% (30 substitutions) between the Ben Lomond and Orford populations to 14.7% (45 substitutions) between the Clarence Lagoon and Ben Lomond sequences (Table 3.1). The mean sequence divergence between the populations was 12.2%. The topology of both the parsimony (Figure 3.4) tree indicated that the Clarence Lagoon and Orford samples were most similar, while the Ben Lomond sequence was the most divergent.

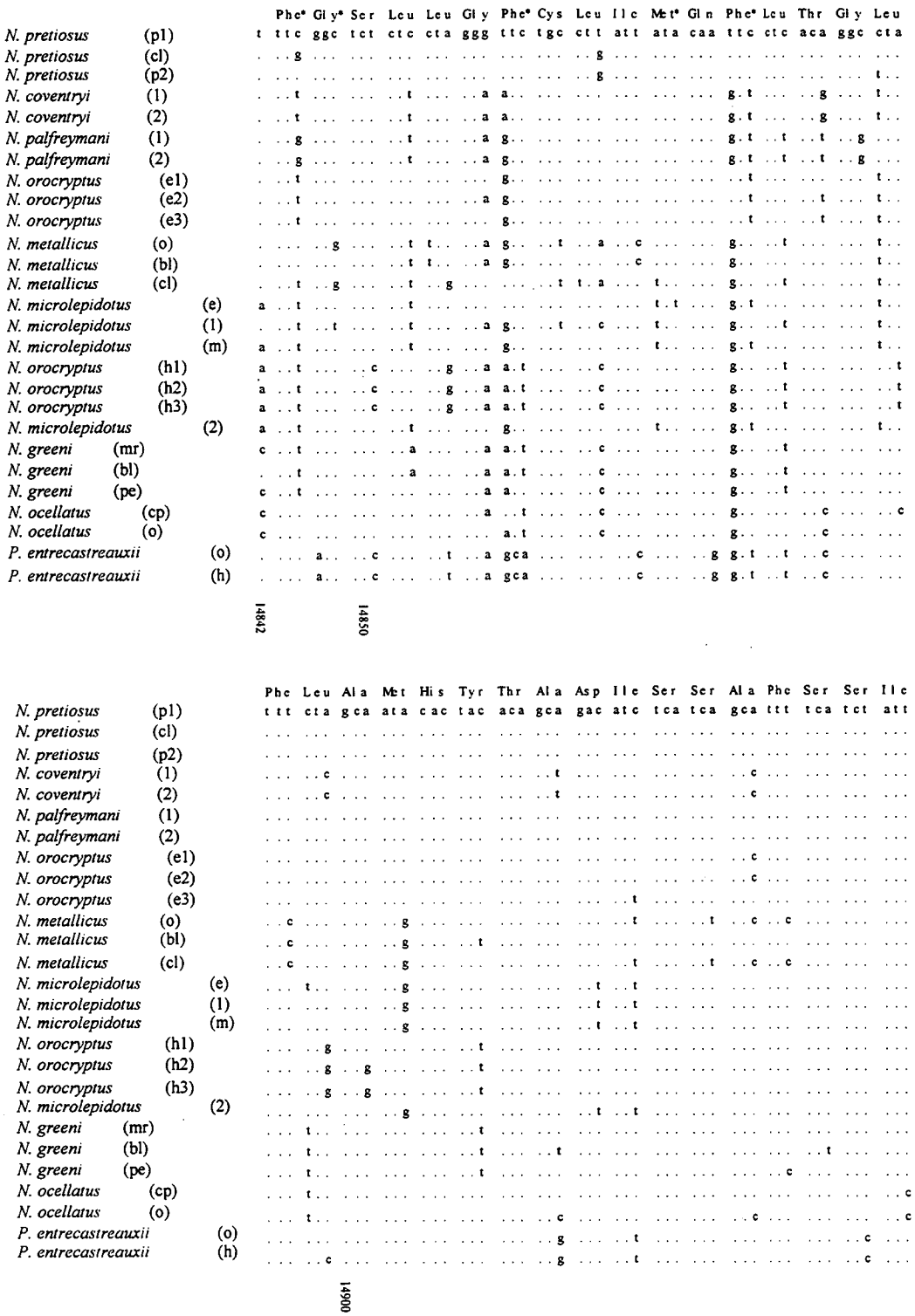


Figure 3.2 Partial cytochrome *b* nucleotide base sequence obtained from 8 species of *Niveoscincus* and *Pseudemoia entrecastreauxii*. The sequences depicted correspond to the light (non-coding) strand of the gene, recorded in the 5' to 3' direction. Dots indicate sequence identity with reference taxon, *Niveoscincus pretiosus*. The numbers at the bottom of the sequence represent the corresponding nucleotide positions within the human mitochondrial genome. The amino acid coding is listed above each codon, with those residues that differ among taxa distinguished by asterisks. In such instances, the residues listed correspond to those observed in the reference taxon.

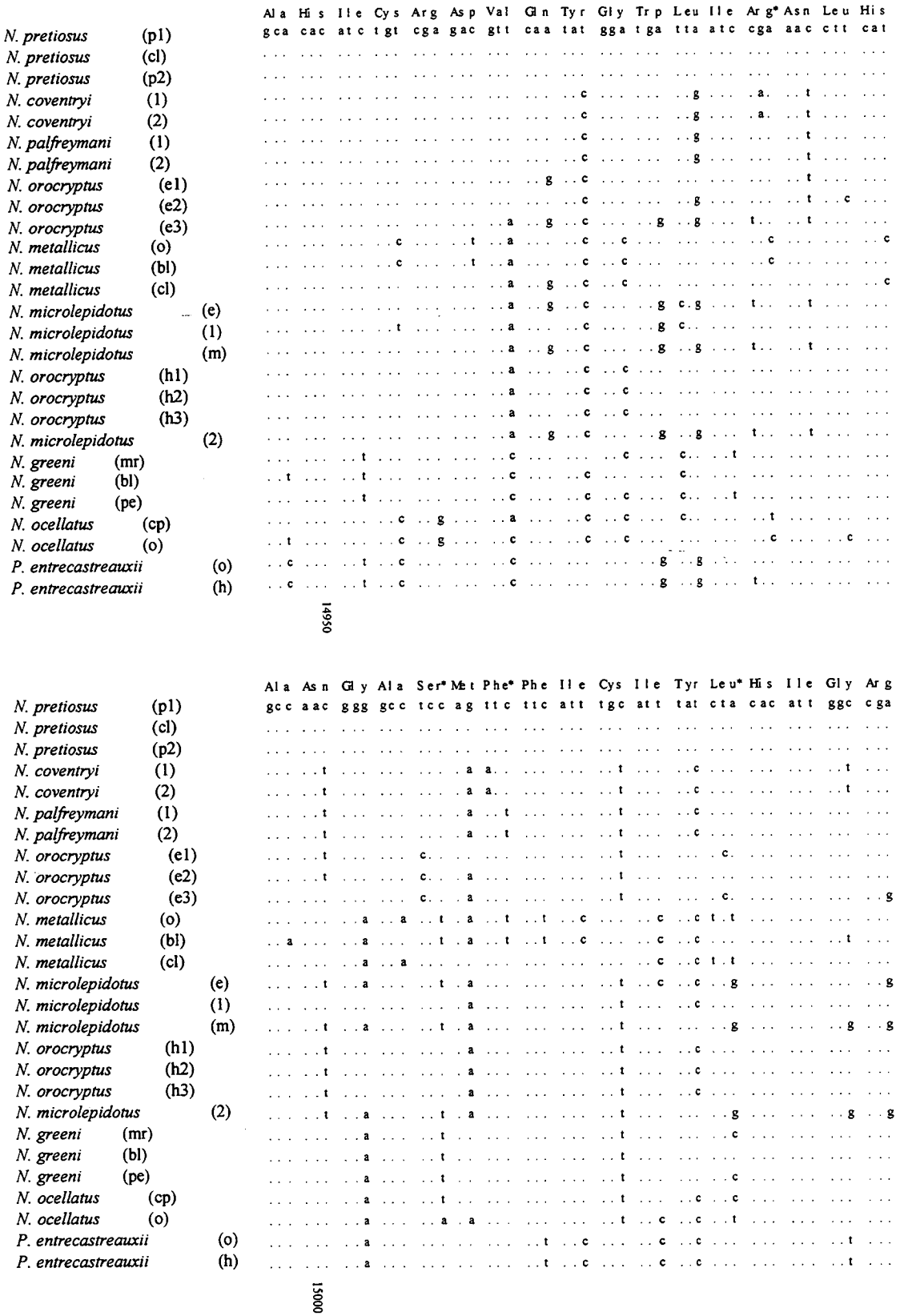


Figure 3.2 Continued.

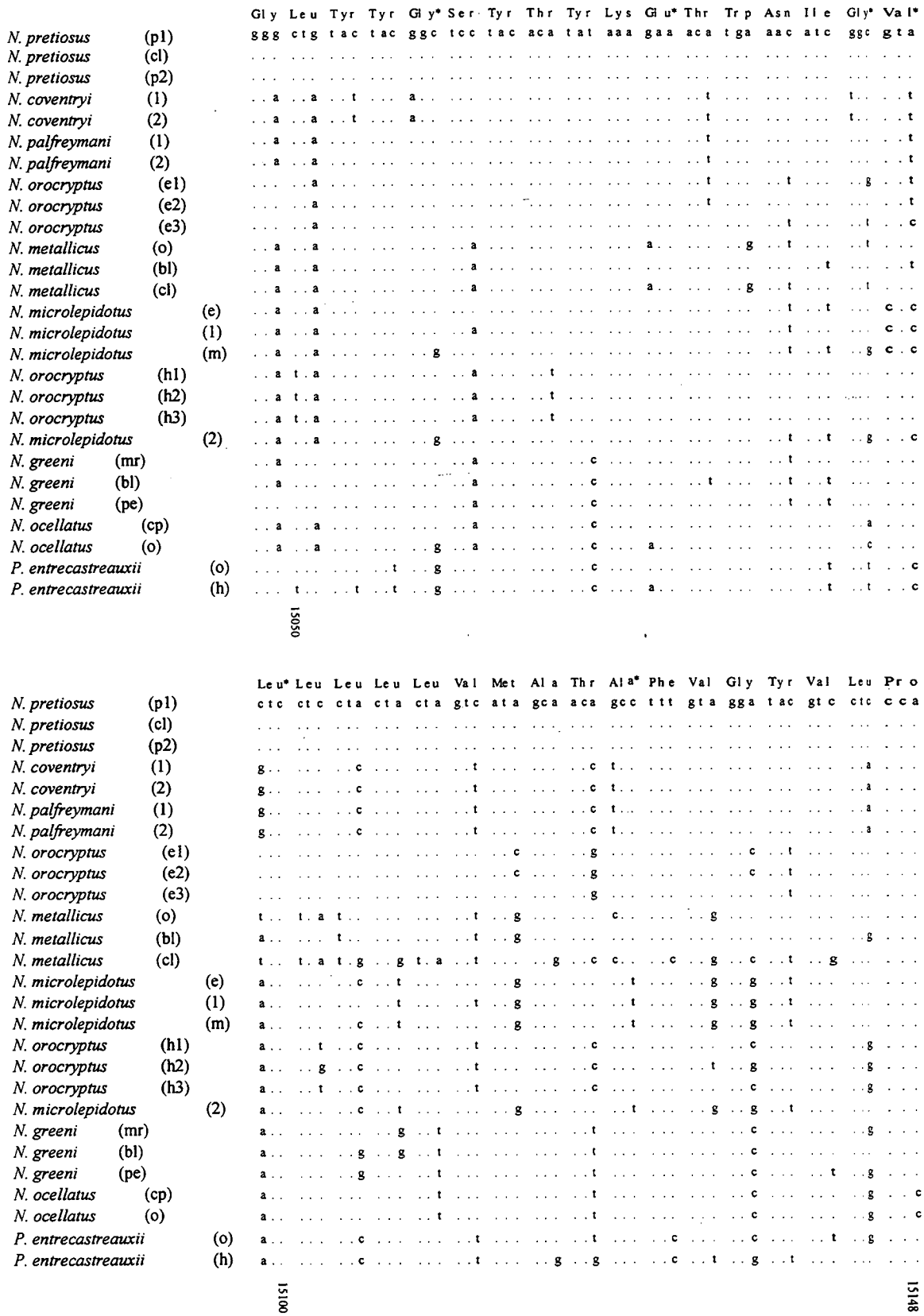


Figure 3.2 Continued.

Niveoscincus microlepidotus populations

Four cytochrome *b* sequences from three populations (Mt Eliza, Mt Hartz and Mt Wellington) of *N. microlepidotus* were analysed (Table 3.1). Pairwise sequence divergence ranged from 2.9% (9 substitutions) between the sequences from Mt Wellington and Mt Eliza to 8.5% (26 substitutions) between the Mt Eliza and Mt Hartz sequences. The genotypes differed by a mean of 4.9%. The topology of both the parsimony (Figure 3.4) and the neighbour-joining (Figure 3.5) trees indicated that the Mt Wellington and Mt Eliza samples were most similar and were divergent from the two Mt Hartz samples.

Niveoscincus greeni populations

A substantial level of intraspecific diversity was detected between *N. greeni* populations. Pairwise sequence divergences ranged from 2.9% (9 substitutions) between the Mt Rufus and Mt Pelion East populations to 4.9% (15 substitutions) between the Ben Lomond and Mt Pelion East sequences (Table 3.1). The mean sequence divergence between the populations was 3.8%. The topology of both the parsimony (Figure 3.4) and the neighbour-joining (Figure 3.5) trees indicated that the Mt Rufus and Mt Pelion East samples were most similar and also divergent from the Ben Lomond sequence.

Niveoscincus ocellatus populations

A high level of intraspecific diversity was detected between the two populations of *N. ocellatus*. The pairwise sequence divergence between the Central Plateau and Orford populations was 9.1% (28 substitutions) (Table 3.1). The topology of both the parsimony (Figure 3.4) and the neighbour-joining (Figure 3.5) trees indicated that the Orford sample was the most divergent.

3.3.3 Interspecific variation in *Niveoscincus*

This analysis included 25 *Niveoscincus* sequences, representing all eight identified species, and 2 samples of *Pseudemoia entrecasteauxii* as an outgroup. Interspecific sequence divergence in *Niveoscincus* ranged from 6.8% (21 substitutions) between *N.*

pretiosus and *N. orocryptus* (Mt Eliza) to 23.1% (71 substitutions) between *N. metallicus* and *N. coventryi.*

An unweighted analysis produced 11 equally parsimonious trees. A strict consensus of these eleven trees showed that all populations were grouped according to accepted species except for one population of *N. metallicus* which was separated from the other populations. *Niveoscincus orocryptus* (Mt Hartz), *N. greeni* and *N. ocellatus* were supported as a monophyletic clade in the strict consensus (Figure 3.3).

Weighting (4:1) resulted in a single most-parsimonious tree whose topology was unchanged with further attempts at successive weighting (Figure 3.4). *Niveoscincus* is resolved as being monophyletic. The boot-strap values obtained place a high level of confidence in grouping the populations of each species, except for the two samples of *N. orocryptus* which are clearly separated. *Niveoscincus orocryptus* from Mt Eliza appears to be a sister species to *N. pretiosus*, while *N. orocryptus* from Mt Hartz is more closely related to the alpine species *N. greeni*. There are boot-strap values below 70 towards the base of the tree.

The phylogenetic analysis divides *Niveoscincus* into two main clades. *Niveoscincus ocellatus, N. greeni* and *N. orocryptus* from Mt Hartz group together and are separated from the remainder of the genus. The bootstrap values at this level show that this division is well supported (Figure 3.4). The remainder of the species then form four groups: *N. coventryi; N. palfreymani; N. pretiosus* plus *N. orocryptus* from Mt Eliza; and *N. metallicus* plus *N. microlepidotus*. The bootstrap values at this level indicate some uncertainty about this part of the topology (Figure 3.4).

The topology of the neighbour-joining tree (Figure 3.5) is largely the same as the most parsimonious tree. *Niveoscincus* is supported as a monophyletic genus and is divided into two main groups, as with the previous analysis. The main difference involved the placement of the *N. metallicus/N. microlepidotus* clade. On the neighbour-joining tree, unlike the most parsimonious tree, this clade is grouped with *N. orocryptus, N. greeni* and *N. ocellatus.*

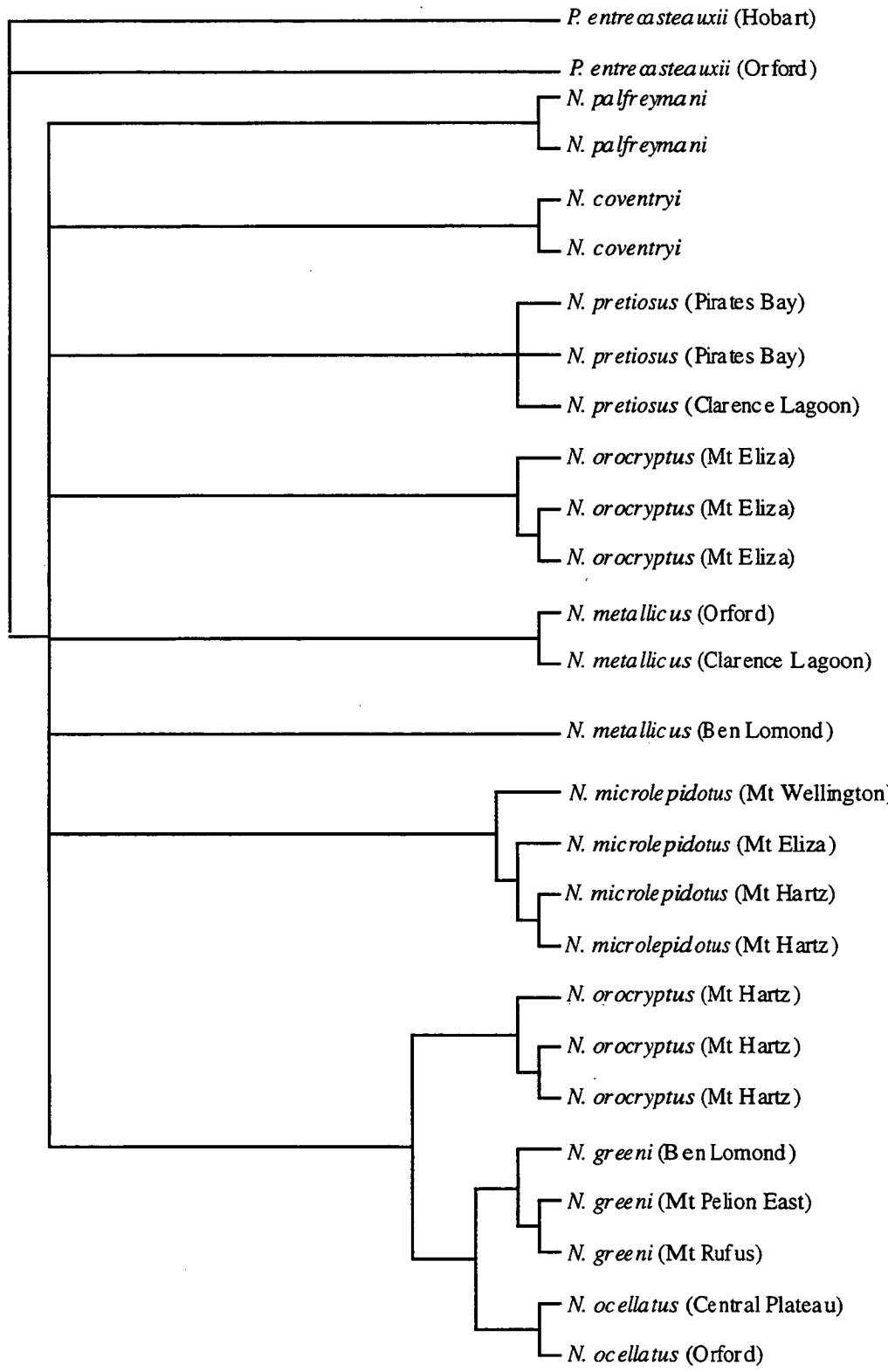


Figure 3.3 Unweighted strict consensus of eleven most parsimonious trees (344 steps) based on 307 bp of cytochrome *b* sequence. The analysis included the 8 species of *Niveoscincus* and was rooted with the outgroup *Pseudemoia entrecasteauxii*.

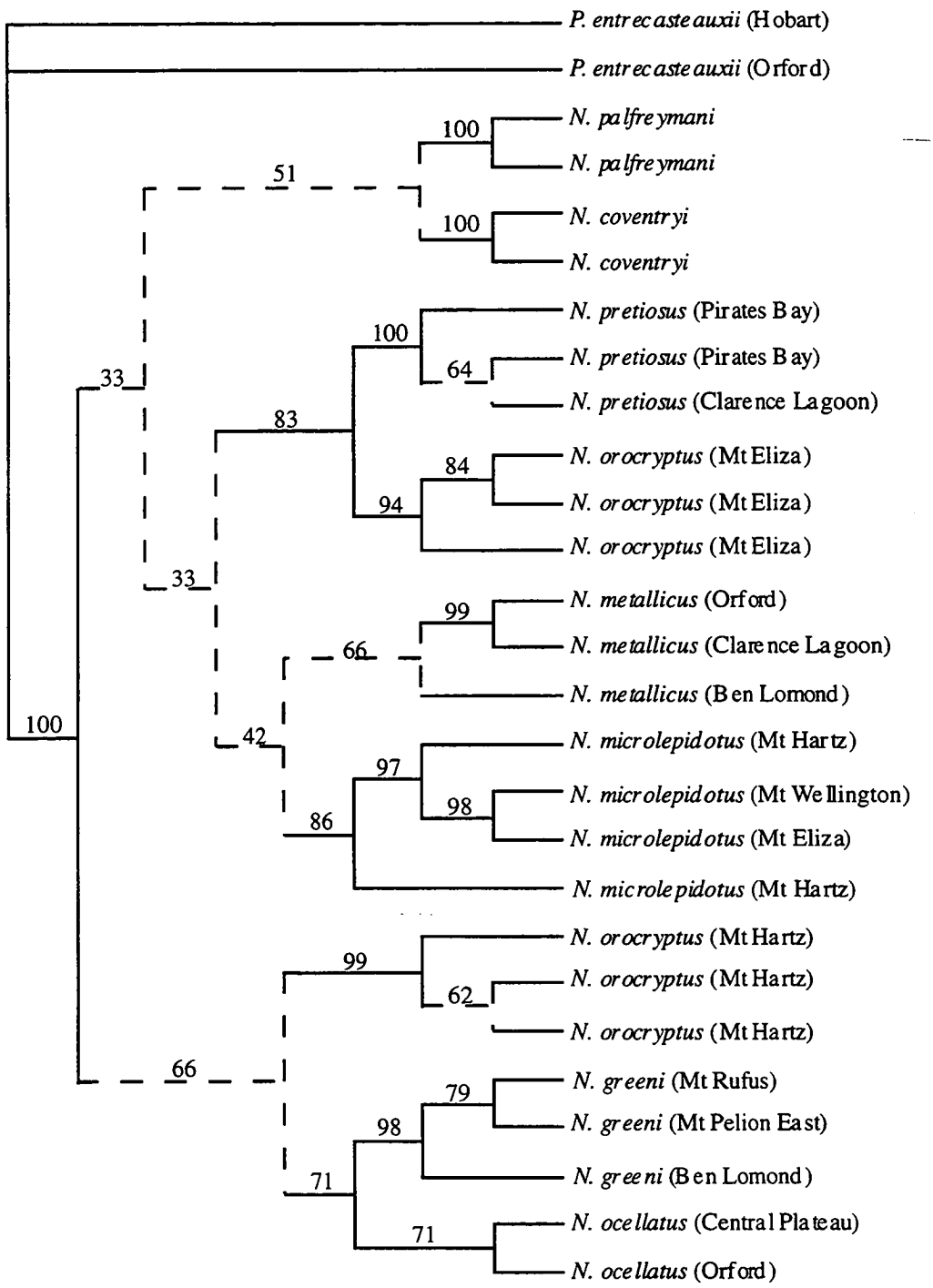


Figure 3.4 Parsimony bootstrap tree (732 steps) based on 307 bp of cytochrome *b* sequence. The analysis included 8 *Niveoscincus* species and the outgroup *Pseudemoia*. TV:TI weight of 4:1. Values at branch points indicate bootstrap values (1000 replicates) with estimates less than 70% shown by dashed lines.

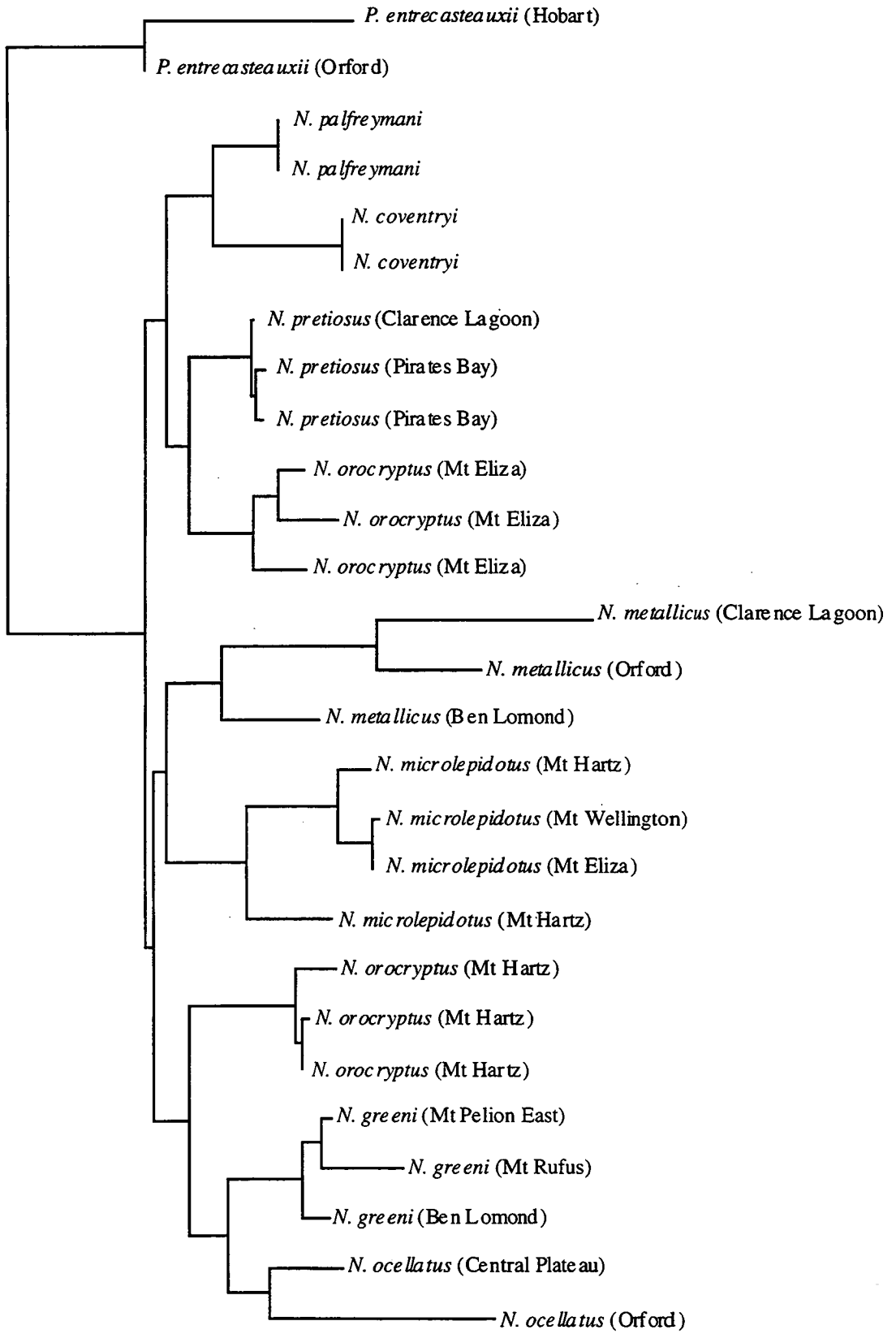


Figure 3.5 Neighbour-joining tree based on a 307 bp of cytochrome *b* sequence. The analysis included 8 *Niveosincus* species and was rooted with the outgroup *Pseudemoia entrecasteauxii*. Distances were calculated with the maximum likelihood algorithm (Felsenstein, 1988).

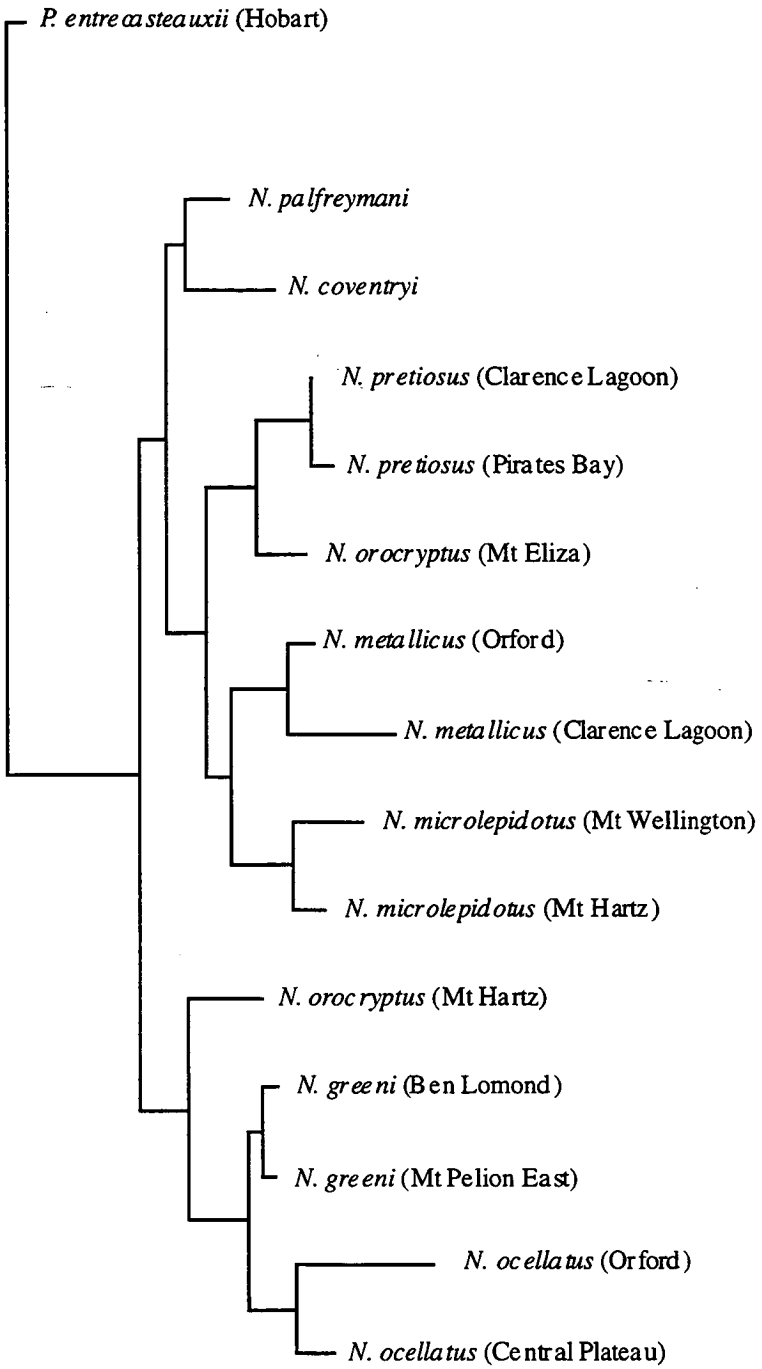


Figure 3.6 Parsimony phenogram (491 steps) to be used in comparative analysis based on 307 bp of cytochrome *b* sequence. The analysis included 8 *Niveoscincus* species and the outgroup *Pseudemoia entrecasteauxii*. TV:TI weight of 4:1.

3.3.4 Phylogeny to be used in comparative analysis

Two populations each for *N. metallicus, N. ocellatus, N. greeni, N. microlepidotus, N. pretiosus* and *N. orocryptus* and one population each of *N. coventryi* and *P. entrecasteauxii* were studied in terms of their ecology, behaviour, morphology and

performance abilities for the comparative analysis. Consequently, the phylogenetic analysis was repeated to include just these populations (Figure 3.6). A weighted (4:1) parsimony analysis was used. The topology of the single most parsimonious tree was the same as that in Figure 3.4. *Niveoscincus palfreymani* remained in this analysis as the topology of the tree changed significantly when it was excluded. The topology and the branch lengths from this tree were used in the comparative analysis of Chapter 8.

3.4 Discussion

The application of molecular techniques in systematic and evolutionary studies has been critical for the determination of phylogeny and taxonomy in traditionally problematic organisms (Densmore and White, 1991). *Niveoscincus* has proved to be a difficult phylogeny to determine. The species are similar morphologically and there is less than 10 albumin ID units difference in the whole genus (Hutchinson *et al.*, 1991). These small albumin ID values are close to the repeatability error of the technique and are subject to the statistical problem of minimal albumin divergence within the group. Consequently, this technique could not be used to establish relationships among the species. Similarly, allozyme electrophoresis, as was discussed in the introduction to this chapter, was also unable to resolve the genetic relationships among the species of *Niveoscincus*. Similar problems have been encountered in other ectotherms, such as the salamander family Salamandridae, where previous interpretations of the evolutionary radiations were based on ecology and functional morphology (Titus and Larson, 1995). However, phylogenetic analyses based on molecular sequencing data permitted a reevaluation of the adaptive hypotheses. The current study found that there was enough sequence variation (6.8 - 23.1%) of the cytochrome *b* gene within *Niveoscincus* to allow satisfactory analysis. This provided a molecular phylogeny of the genus and also the opportunity to examine possible patterns of evolutionary radiation and speciation.

The study of species undergoing varying degrees of divergence may shed light on the events leading to speciation (Lawson *et al.*, 1991). Considerable interest has centred around the degree to which phylogeographic patterns and animal taxa are related to historical changes in the environment (Brooks, 1985; Joseph, *et al.*, 1995; Zamudio *et al.*, 1997). Addressing this issue at a molecular level requires an understanding of the sequence diversification among and within lineages and its concordance with environmental shifts that may have occurred at the same scale (Riddle, 1995). If these historical patterns can be teased apart from current dynamics, they can be used, along with information on past climatic and geological events, to reconstruct a picture of the historical biogeography of species (Shaffer and McKnight, 1996). This approach can be especially rewarding in areas such as Tasmania where the events connected with Pleistocene glaciations have been well studied.

The bootstrap values on the most parsimonious phylogeny of *Niveoscincus* indicated a high level of confidence in grouping the species together. However, the bootstrap values towards the base of the tree were low. This uncertainty in how the lineages are grouped may indicate that a period of rapid cladogenesis occurred in the past. However, the large interspecific divergences in *Niveoscincus* suggest that most speciation or divergence events occurred well before the climatic extremes of the Pleistocene.

A late Tertiary orgin of the genus is suggested if a rate of 2% sequence divergence per million years is used. Molecular datings, such as this, have always been very appealing because they may be used when no other information, such as stratigraphy and palaeontology, are available for time estimates (Caccone *et al.*, 1997). However, the use of molecular data as an indicator relies on the assumption that molecular divergence is linear over time. This issue has been controversial since the introduction of the molecular clock or rate-constancy hypothesis (Zuckerkandl and Pauling, 1965).

A number of studies have challenged the rate-constancy hypothesis, showing that nucleotide substitution rates vary dramatically within gene regions and among divergent taxonomic groups, in both the nuclear and mitochondrial genome (eg. Wu and Li, 1985; Bulmer *et al.,* 1991; Martin *et al.*, 1992; Caccone *et al.*, 1997). However, the substitution rate of 1-2% per million years continues to be used frequently for mtDNA. This figure has been obtained from primate mtDNA (Brown *et al.*, 1982) and is now commonly used for all vertebrates. It has been found that differences in divergence rates exist not only among different genes but also for the same gene between vertebrate groups (eg. Meyer and Wilson, 1990; Martin *et al.*, 1992; Caccone *et al.*, 1997). However, this divergence rate has been used successfully in other in molecular studies of lizards (e.g. Thorpe *et al.*, 1994). Consequently, it is likely that sequence divergence in *Niveoscincus* does not vary significantly from the 2% substitution rate.

A divergence rate of 2% per million years would indicate that radiation within *Niveoscincus* occurred between 3 and 10 million years ago. This coincides with a period of dramatic changes in the Tasmanian vegetation. Macphail *et al.* (1991) provided strong palynological evidence for the existence of a cool-adapted flora in Tasmania during the Late Tertiary. The forest edge habitat at high altitudes may represent the environment in which the alpine/subalpine flora evolved. Woody shrubs and herbs increased in their dominance, resulting in higher light intensities at ground level (Macphail *et al.*, 1991). The phylogeny from cytochrome *b* indicates that the separation of the heath dwelling species *N. orocryptus* (Mt Hartz) was the first divergence of extant species in *Niveoscincus*. It is possible, therefore, that *Niveoscincus* evolved in association with the development of the open alpine/subalpine flora in the late Tertiary.

The divergence of the extant *Niveoscincus* species may have occurred between 3 - 10 million years ago, possibly associated with the opening of the forests and the

associated development of open woodlands, grasslands and heathlands. Tasmania's climate was becoming much cooler and drier at this time (Greenwood, 1994).

The current biogeographic patterns in *Niveoscincus* may be explained by the vicariance or "refuge" hypothesis, which would suggest a relatively recent or partial restriction of gene flow. Vicariant biogeographic analyses focus on congruent patterns among monophyletic assemblages of species, addressing the role of ancient geological events in shaping biological distributions on a broad spatial scale (Lamb *et al.*, 1992). An example of this is the biogeography of Tasmanian flora, which has been affected by the Pleistocene glacial events. Palaeoclimatological and palynological evidence has indicated that repeated contractions and expansions of habitat types occurred with the Pleistocene glacial fluctuations (Greenwood, 1994). Consequently, it is probable that the ancestral populations of *Niveoscincus* were subjected to expansions and contractions during the Pleistocene glaciations in association with the habitats in which they occurred.

Niveoscincus orocryptus from Mt Hartz forms a clade with *N. greeni* and *N. ocellatus*. The distributions of these species suggests that speciation may have occurred through vicariance events associated with glaciations. *Niveoscincus orocryptus* is found in south-western Tasmania, while *N. greeni* has a north-eastern distribution, extending into central Tasmania and *N. ocellatus* occurs mainly in eastern Tasmania. During the extreme glacial periods it is believed that much of central Tasmania was covered by glacial ice-sheets and vegetation was restricted to coastal areas (Greenwood, 1994). Thus, it is possible that an ancestral species was restricted during glacial periods to refuges in southern and northern Tasmania, with subsequent genetic divergence leading to speciation.

Kirkpatrick and Fowler (1996) suggest that since the last glacial period Tasmania has changed from a peninsula largely covered by alpine vegetation, grassland and grassy woodland, to an island largely covered by forest. Alpine and grassland areas were

more widespread and contiguous than they are today, while eucalypt forest was restricted to northern coastal areas. It is likely that the species of *Niveoscincus* contracted to refugia during Pleistocene glacial periods, with allopatric divergence among species occurring. These results suggest that historical contractions of vegetation around the glacial ice-sheets have promoted substantial genetic differentiation within species.

The high degree of intraspecific sequence divergence in the genus *Niveoscincus*, up to 14.7%, has been observed in other species of lizards. High levels of nucleotide variation, ranging from 0.1% to 11.9%, among populations of the short-horned lizards (*Phrynosoma douglasi*) (Zamudio *et al.*, 1997). Similarly, sequence divergence in the prickly skink (*Gnypetoscincus queenslandiae*) ranged from 0.28% to 8.1% (Joseph *et al.*, 1995).

Genetic population structure in most organisms is determined by a combination of current population dynamics and historical patterns of gene flow among populations (Phillips, 1994; Templeton *et al.*, 1995). The study of intraspecific biogeography involves the joint consideration of the phylogenetic and geographic distributions of populations and is valuable for understanding both macroevolutionary and microevolutionary processes (Routman *et al.*, 1994). DNA sequencing is often more informative than other techniques, such as morphological data, because, for most species, populations are closely related.

Niveoscincus orocryptus at the Hartz Mountains is a population which is very similar morphologically to *N. microlepidotus* and allozyme electrophoresis was not able to separate these species confidently (Hutchinson and Schwaner, 1991). However, the sequencing data have distinguished these species at the Mt Hartz site and have also separated the *N. orocryptus* populations from Mt Hartz and Mt Eliza. This molecular analysis indicates that the Mt Eliza population of *N. orocryptus* is more closely related to *N. pretiosus* while the Mt Hartz population is related to *N. greeni* and *N. ocellatus*.

For this reason the rest of this thesis will treat these two populations separately. However, these two populations may not be separate species as hybridisation at one of the sites could have caused the fixation of alleles within the population. More research needs to be conducted to determine the taxonomic status of these populations.

It cannot be assumed that the radiation of species in *Niveoscincus* is solely a result of vicariance. Sympatric speciation may also have occurred, involving adaptation to factors such as microhabitat variation. This has occurred many times in other clades of lizards. For example, lizards of the family Xantusiidae have a highly discontinuous range, with disjunctions as great as 100 km (Bezy and Sites, 1987). Morphological similarity and divergence among these isolated populations appears to be correlated with microhabitat, suggesting that selection may constitute both the major cohesive as well as disruptive force in the group. Microhabitat use in *Niveoscincus* is examined further in Chapter 4.

The suggestion that a single species may have given rise to four modern lineages during the Pleistocene glaciations (Hutchinson and Schwaner, 1991) does not agree with the extent of divergence which was found in this study between the species of *Niveoscincus*. It is more probable that a heath dwelling species in the late Tertiary gave rise to the modern lineages of *Niveoscincus*. In future research I will be sequencing further genes to provide further support for this hypothesis and to strengthen the confidence of the phylogeny obtained by sequencing cytochrome *b*.

CHAPTER FOUR
MICROHABITAT OCCUPATION

4.1 Introduction

Ecomorphological studies usually attempt to link the structure and function of organisms to relevant factors within the environment (Wainwright, 1991; Losos and Miles, 1994). Ecomorphological hypotheses assume that differences in morphology translate into differences in performance capability, which, in turn, result in differences in ecology or behaviour. The habitat matrix model (Moermond, 1979; Pounds, 1988) predicts that morphology and behaviour reflect interspecific microhabitat differences. Much of the research in ecological morphology is concerned with how organisms have evolved in response to environmental circumstances and biologists comparing species have often noted correlations between morphology and habitat (Garland and Losos, 1994). Increasingly, ecologists are realising that evolutionary history can be a major factor in determining present-day patterns in microhabitat use.

The relationships between morphology, microhabitat use and locomotor behaviour are complex. Losos (1990a) found that morphology, performance abilities, and ecology and behaviour are closely related in the lizard genus *Anolis*. Morphologically similar species of *Anolis* use similar microhabitats (Losos, 1990b). Particular locomotor behaviours are favoured in different microhabitats where species evolve the morphology appropriate for a given locomotor mode.

A common feature in assemblages of lizards is the tendency for divergence in microhabitat use to occur (Schoener, 1974; Miles, 1994). This has been attributed to many factors, including dietary requirements, thermal requirements or behavioural and morphological differences between species. This chapter provides a quantitative analysis of microhabitat occupation in the study species of *Niveoscincus* which will allow a comparative study of the relationships between microhabitat occupation,

behaviour, morphology and performance abilities (Chapter 8). Microhabitat use has been described in many studies including both desert lizards (eg. Pianka, 1975; Pianka, 1980; Barbault and Maury, 1981; Shenbrot *et al.*, 1991) and temperate species (eg. Dent and Spellerberg, 1987; Scheibe, 1987; Adolph, 1990). However, very few studies have used this information to investigate the relationships between performance, morphology, ecology and behaviour (Losos, 1990).

Previously, the occupation of microhabitats has not been quantified in most species of *Niveoscincus*. Microhabitat use by *N. metallicus* and *N. microlepidotus* was investigated at a sub-alpine site on Mt Wellington (Melville and Swain, 1997a), but existing descriptions of the other species have been very generalised, providing only qualitative summaries of broad habitat preferences (Hutchinson *et al.*, 1989; Rawlinson, 1974). Consequently this study provides the first opportunity to conduct a quantitative investigation of microhabitat occupation by all *Niveoscincus* species and *Pseudemoia entrecasteauxii*, while also characterising the separation of microhabitat use between these species.

4.2 Materials and Methods

4.2.1 Field work

The data were recorded by starting at a randomly determined location at each field site (see Chapter 2) and moving back and forth across the site to ensure coverage of the entire range of microhabitats available. When an undisturbed lizard was sighted the species and, if determined, the sex were recorded immediately. Capture of the lizard was then attempted and, if caught, the sex of the lizard was confirmed. The number of lizards observed for this study varied between field sites. The total number of specimens for which microhabitat variables were recorded at each site ranged from 49

to 65. Whether or not a lizard was captured, the environmental and structural characteristics of the microhabitat were recorded. These included:

1. canopy type (CT): eucalypt, rainforest or other;
2. percentage of canopy in a 3 m^2 radius surrounding lizard (CC);
3. canopy height in metres (CH);
4. the surface on which the lizard was basking (BS): rock, litter, ground, log, branch or tree trunk;
5. undergrowth vegetation type (VT): trees (>2 m), shrubs (1-2 m), shrubs (<1 m), ground cover or grass;
6. distance to the nearest vegetation in centimetres (NV);
7. percentage of vegetation in a 3 m^2 radius surrounding lizard (VC);
8. vegetation height in metres (VH);
9. substrate type (ST): litter, rock, gravel, soil, and combinations of these; and
10. visual estimation of substrate wetness (SD): measured on a scale of 1 - 6 (1 = dry substrate, 6 = water sitting on surface of substrate).

4.2.2 Statistical analysis

A principal components analysis (PCA) was used to reduce these ten environmental and structural variables to a smaller number of uncorrelated components that describe the underlying dimensions in the microhabitat data (FACTOR procedure of SYSTAT, Wilkinson *et al.*, 1992). The principal components were extracted from the correlation matrix of the raw data. This matrix had the advantage of being independent of scales of variable measurement (Tabachnick and Fidell, 1989). The data were not transformed prior to analysis as many of the values for the distance to vegetation and shelter were zero and performing a log transformation would have resulted in the loss of valuable data. Thus it is possible that the assumption of linearity was violated (James and McCulloch, 1990). However, departures from linearity are not usually great enough to invalidate a PCA (Pimentel, 1979). The number of principal components (henceforth PCs) utilised in the analysis was determined by using the scree test of eigenvalues

plotted against factors, maximising the adequacy of extraction. PC axes were named by the correlations of the original variables to the PC: correlations with absolute values of greater than 0.5 were considered significant (Tabachnick and Fidell, 1989).

Rotation of data is usually used to improve the interpretability of the solution. Rotation was not used because SYSTAT only offers orthogonal procedures (varimax, quartimax and equamax), which lose validity if PCs are not wholly independent. Microhabitat variables such as the percentage of canopy cover and substrate wetness, which are in separate PCs, would to some degree be dependent upon each other. I believe the results of this analysis were able to be interpreted adequately without rotation.

The mean scores of each axis were calculated for all the *Niveoscincus* populations and the *Pseudemoia entrecasteauxii* population. These values could then be used in the Independent Contrasts analysis in Chapter 8 as measures of microhabitat occupation.

Following the PCA, a direct discriminant function analysis (MGLH procedure of SYSTAT, Wilkinson et *al.*, 1992) was performed on the PC axes of each population, species and ecomorph in order to determine if there was any significant separation along the axes. For the ecomorph analysis the species were grouped according to whether they were ground-dwelling, arboreal or saxicolous. Even though the sample sizes for each species are slightly uneven, there are no particular violations of statistical assumptions (Tabachnick and Fidell, 1989) and sample sizes are large enough to ensure multivariate normality; that is, the microhabitat scores are a random sample of the population. Discriminant function analyses are very sensitive to the inclusion of outliers (Tabachnick and Fidell, 1989). Thus, univariate and multivariate outliers were identified for each species and those that were significant were eliminated before the analysis.

4.3 Results

4.3.1 Occupation of microhabitat

The principal components analysis was originally performed separately on both sexes of each species; however, since no significant differences were found between sexes the data were pooled.

The PCA that incorporated two factors accounted for 61.675% of the variance of the raw data (Table 4.1). The number of factors used in the analysis was determined using a scree test (Figure 4.1), where the change in slope indicated the number of factors which should be used.

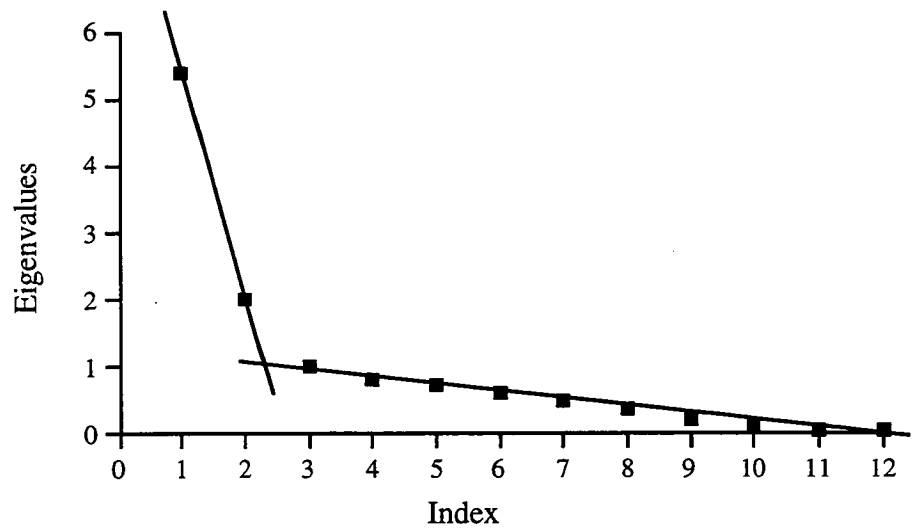
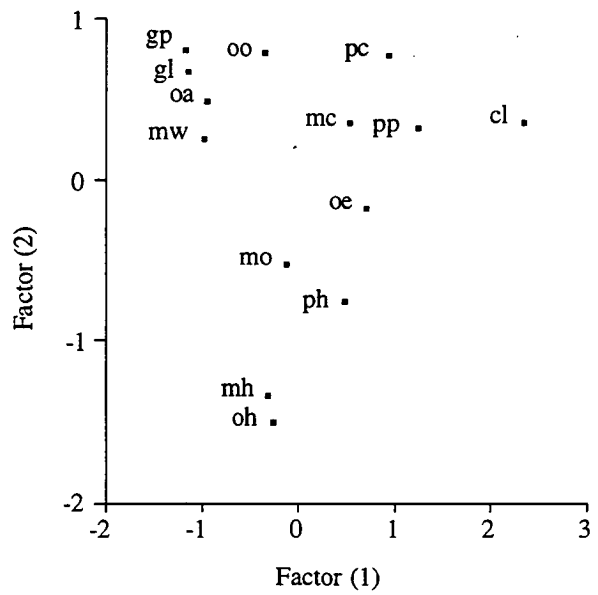


Figure 4.1 Scree plot of eigenvalues from principal components analysis.

The first PC yielded a strong positive correlation between the vegetation type, vegetation height, percentage of vegetation cover, substrate wetness, canopy type, percentage of canopy cover and canopy height. A strong negative correlation with the basking surface was revealed on the first PC axis (Figure 4.2). Thus, the PC 1 axis described a vegetation and substrate gradient in which high PC scores denoted a microhabitat surrounding the basking sites that was characterised by high, dense vegetation and damp substrates and negative PC scores denoted open, rocky areas with

little or no shade. The second PC axis showed strong negative correlations with the percentage of vegetation cover and substrate type and strong positive correlations with the distance to the nearest vegetation (Figure 4.2). This represents a scale of ground cover vegetation in which low PC 2 scores denoted extensive areas of ground-cover vegetation with very little exposed substrate and high scores denoted limited vegetation at ground level.



cl - *N. coventryi* (Mt St Leonards)
gl - *N. greeni* (Ben Lomond)
gp - *N. greeni* (Mt Pelion East)
mc - *N. metallicus* (Clarence Lagoon)
mo - *N. metallicus* (Orford)
mh - *N. microlepidotus* (Mt Hartz)
mw - *N. microlepidotus* (Mt Wellington)
oa - *N. ocellatus* (Lake Augusta)
oo - *N. ocellatus* (Orford)
oe - *N. orocryptus* (Mt Eliza)
oh - *N. orocryptus* (Mt Hartz)
pc - *N. pretiosus* (Clarence Lagoon)
pp - *N. pretiosus* (Pirates Bay)
ph - *P. entrecasteauxii* (Hobart)

Figure 4.2 The first two principal components axes of the *Niveoscincus* species and *Pseudemoia entrecasteauxii*.

Only PC1 was to be used in the independent contrasts analysis (Chapter 8) because it accounted for the largest percentage of the variance of the raw data (Table 4.1) and it represented the largest section of the structural microhabitat. PC2 only represented the vegetation structure at ground level.

Table 4.1 Correlations of original environmental variables with the first two PC scores for the *Niveoscincus* species and *Psuedemoia entrecasteauxii*

	PC 1	PC 2
Correlations with PCs	BS -0.735 VT 0.932 VH 0.798 SD 0.535 VC 0.526 CT 0.814 CH 0.910 CC 0.897	ST -0.770 NV 0.541 VC -0.702
Percent of variance	45.031	16.644
	n	Score (mean ± se)	Score (mean ± se)
N. coventryi (Mt St Leonards)	51	2.36 ± 0.030	0.35 ± 0.028
N. greeni (Ben Lomond)	55	-1.13 ± 0.016	0.66 ± 0.049
N greeni (Mt Pelion East)	50	-1.17 ± 0.013	0.79 ± 0.041
N. metallicus (Orford)	62	-0.10 ± 0.056	-.052 ± 0.080
N. metallicus (Clarence Lagoon)	62	0.56 ± 0.057	0.35 ± 0.028
N. microlepidotus (Mt Hartz)	55	-0.30 ± 0.027	-1.34 ± 0.108
N. microlepidotus (Mt Wellington)	49	-0.98 ± 0.032	0.25 ± 0.068
N. ocellatus (Lake Augusta)	61	-0.96 ± 0.025	0.48 ± 0.081
N. ocellatus (Orford)	52	-0.33 ± 0.038	0.78 ± 0.051
N. orocryptus (Mt Eliza)	62	0.70 ± 0.065	-0.18 ± 0.163
N. orocryptus (Mt Hartz)	65	-0.26 ± 0.028	-1.51 ± 0.087
N. pretiosus (Clarence Lagoon)	56	0.93 ± 0.022	0.76 ± 0.040
N. pretiosus (Pirates Bay)	49	1.25 ± 0.048	0.31 ± 0.078
P. entrecasteauxii (Hobart)	52	0.50 ± 0.043	-0.76 ± 0.058

Of the original 785 lizards recorded, six were identified as outliers and and subsequently removed from the analysis. Two of the statistical outliers were *N. pretiosus* from Clarence Lagoon that had been observed basking in an open area on a rock. Two other outliers were *Pseudemoia entrecasteauxii* basking on a small rocky outcrop at the Hobart field site. One of the remaining outliers was a *N. metallicus* that

was observed basking in the full sun on a small outcrop of rocks at the Orford site. The remaining outlier was a *N. greeni* basking in full shade under a small *Eucalyptus coccifera*. Assumptions of linearity and normality were not violated for the remaining 779 lizards (Table 4.1) .

A discriminant function analysis revealed interspecific differences in the PC scores on both PC 1 and 2 (Table 4.1). The highest mean score on PC 1 was yielded by *N. coventryi* (Mt St Leonards) and the lowest mean score by *N. greeni* (Mt Pelion East). There were significant differences between all species on PC 1 ($F_{8,770} = 580.36$, $p<0.001$). On PC 2 the highest mean score was recorded by *N. greeni* (Mt Pelion East), while *N. orocryptus* (Mt Hartz) had the lowest mean score. There were significant differences between species on PC 2 ($F_{8,770} = 85.76$, $p<0.001$).

The populations of *N. metallicus* ($F_{1,122} = 72.36$, $p<0.001$), *N. orocryptus* ($F_{1,125} = 86.39$, $p<0.001$), and *N. microlepidotus* ($F_{1,102} = 261.94$, $p<0.001$) showed significant differences on PC 1. There were no significant differences between the populations of *N. greeni, N. ocellatus* and *N. pretiosus*. On PC 2 there were significant differences between the populations of *N. metallicus* ($F_{1,122} = 73.90$, $p<0.001$) and *N. microlepidotus* ($F_{1,102} = 148.14$, $p<0.001$), while there were again no significant differences between the populations of *N. greeni, N. ocellatus* and *N. pretiosus.*

Some of the species which were recorded at the same field sites show significantly different scores along PC1. For example, *N. metallicus* and *N. ocellatus* at the Orford field site occupy significantly different microhabitats as shown by PC1 ($F_{1,112} = 7.73$, $p = 0.006$). A similar situation occurs at Clarence Lagoon with *N. metallicus* and *N. pretiosus* ($F_{1,114} = 35.77$, $p<0.001$). However, *N. microlepidotus* and *N. orocryptus* at Mt Hartz show no significant differences on PC1 ($F_{1,118} = 0.15$, $p = 0.698$).

The species were grouped together according to ecomorph type for further analysis: whether they were ground-dwelling, arboreal or saxicolous. *Niveoscincus greeni, N.*

microlepidotus, N. ocellatus and *N. orocryptus* (Mt Hartz) were classified as saxicolous species. *Niveoscincus metallicus, N. coventryi* and *Pseudemoia entrecasteauxii* were grouped together as ground-dwelling lizards, and *Niveoscincus pretiosus* and *N. orocryptus* (Mt Eliza) formed the arboreal group. A direct discriminant function analysis was performed on these three groupings, using the two PC axes as predictors of the occupation of basking sites.

The discriminant function analysis showed that the microhabitat PC scores for the ecomorph types differed on both PC 1 ($F_{2,776} = 589.37$, $p<0.001$) and PC 2 ($F_{2,776} = 8.33$, $p<0.001$). On PC 1, Fisher's LSD post hoc test showed that mean scores for all ecomorphs differed significantly from each other ($p<0.001$).

4.4 Discussion

4.4.1 Microhabitat occupation

Niveoscincus coventryi

Niveoscincus coventryi has previously been studied in the central highlands of Victoria and described as a cryptic species associated with deep layers of litter and vegetation (Rawlinson, 1975; Greer, 1982; Brown and Nelson, 1993). Webb (1985) in a study of microhabitat use of some Southeastern Australian skinks found that *N. coventryi* spent 92% of their time in the litter. This is very similar to the findings of this study, where the lizards occupied the deep litter layers on the ground, especially around the base of large *Eucalyptus regnans* trees.

Niveoscincus coventryi occupied the most closed microhabitat of all *Niveoscincus* species. It occupied similar forests to *N. pretiosus*: wet sclerophyll forests with tall dense canopies and tall, thick undergrowth. However, *N. pretiosus* mainly occupied areas where the canopy had been broken by tree falls, while *N. coventryi* was found

throughout the forest. *N. coventryi* was very cryptic, basking in small patches of dappled sunlight.

Niveoscincus greeni

This is the first study to quantify the microhabitat of *Niveoscincus greeni* which has previously been described as a saxicolous species (Rawlinson, 1975; Greer, 1982; Hutchinson and Schwaner, 1991), occupying a similar type of microhabitat to *N. microlepidotus*. The current study supports the previous finding that *N. greeni* is saxicolous, as it was found only in open boulder fields, even when other microhabitats were only metres away.

This species is much more specialised in its microhabitat occupation than *N. microlepidotus*. Over the three years of study *N. greeni* was never seen outside the open boulder fields. These lizards were often observed to move around over small creeping plants which covered some of the rocks but they were never observed in areas where the substrate changed to peat or in dense vegetation. At the Mt Pelion East field site *N. greeni* and *N. microlepidotus* occurred in sympatry but they occupied very different microhabitats. *Niveoscincus greeni* occupied the small patches of boulders, while *N. microlepidotus* was recorded only in the heath and peat areas. This situation of sympatry between *N. greeni* and *N. microlepidotus* only occurs within a small geographical area in central Tasmania because this is the only area where the distribution of the two species overlaps. Sympatry between *N. greeni* and *N. microlepidotus* has been reported previously at Mt Rufus (Hutchinson *et al.*, 1989) but no details of microhabitat occupation were provided. At Mt Pelion East the two species use habitats only metres apart. Interactions between the species were never observed but some form of interference competition is probably occurring since elsewhere, where *N. microlepidotus* is the only species present, it occurs in highest densities in boulder fields (Melville, 1997a)

Niveoscincus metallicus

All previous reports of *N. metallicus* have described this species as a ground dwelling and relatively cryptic species, found in a wide range of habitats (Rawlinson, 1974; Hutchinson and Schwaner, 1991; Melville and Swain, 1997a,b). This study supports the reports that the species is cryptic and ground dwelling in nature; it occupies shaded microhabitats with medium to dense vegetation cover, soil and thick litter.

Niveoscincus metallicus appears to be restricted to a closed microhabitat at the higher altitude site of Clarence Lagoon than at Orford. There was a dense canopy, with more undergrowth and the lizards at this site tended to bask on rocks to a greater extent than the lizards at Orford, despite the fact that there were greater numbers of logs available for basking at Clarence Lagoon. At the Orford field site *N. metallicus* occupies an open microhabitat but is more closely associated with litter layers and ground-cover vegetation. This supports the conclusions of Melville and Swain (1997a) who found that *N. metallicus* occupied a fairly closed microhabitat at a high altitude site on Mt. Wellington.

Niveoscincus metallicus also occupies a significantly different microhabitat to *N. pretiosus* at the Clarence Lagoon site. *Niveoscincus metallicus* occupies more open areas, basking on rocks and to a lesser extent litter and logs, while *N. pretiosus* occupies the thickly forested wet sclerophyll areas of the site which have dense canopy, and extensive shading; *N. pretiosus* were observed almost exclusively on fallen logs and trees. At Clarence Lagoon there are areas of large tree falls which break the canopy and provide large, complex microhabitats with sunny patches for basking. The difference in microhabitat utilisation between *N. metallicus* and *N. pretiosus* may be a result of interference competition, which has been suggested as the cause of ecological differences among species (Talbot, 1979; Toft, 1985). The impact of interspecific competition on microhabitat use is a contentious issue, and has been debated in many studies (eg. Schoener and Gorman, 1968; Pacala and Roughgarden, 1985; Moermond, 1986; Scheibe, 1987) which have concluded that microhabitat separation is a result of

factors other than competition. It is perhaps more likely that microhabitat separation between *N. pretiosus* and *N. metallicus* is a result of specialisation. *N. pretiosus* exhibits behaviour, performance ability and morphology that indicate that it is specialised for moving around on fallen trees, while *N. metallicus* is a ground dwelling species (see following Chapters).

Niveoscincus microlepidotus

The results obtained from the quantitative analysis of microhabitat occupation by *N. microlepidotus* support the existing descriptions of habitat preferences for this species. Hutchinson *et al.* (1989) described *N. microlepidotus* as an alpine species that occurs in large numbers in dolerite boulder fields above 1000 m in southern Tasmania. This study has shown that *N. microlepidotus* has a preference for the open boulder fields, on which it basks. Melville and Swain (1997a) reached the same conclusion in an analysis of microhabitat use by *N. microlepidotus* on Mt Wellington. However, the current study found that *N. microlepidotus* also uses other microhabitats: alpine heaths and sub-alpine woodlands. The lizards do not occupy those areas in the woodlands where dense vegetation, heavy shading, damp soils and deep layers of litter occur. These habitats exist only at the lower end of the species' altitudinal distribution, where the study sites were located.

The only previous study of *N. microlepidotus* (Melville and Swain, 1997a) found that, at the study site on Mt Wellington, basking always occurred on a rock surface, although Hutchinson *et al.* (1989) reported that the species utilises vegetation and logs as basking perches. The present study identified a large difference between microhabitat occupation at the Mt Wellington field site and the Mt Hartz site. The lizards at Mt Hartz occupied the heathland, basking on branches, the top of heath plants, on the ground, on cushion plants and on the few rocks available. These observations suggest that *N. microlepidotus* is a much more generalist species than *N. greeni* which was never observed outside the boulder fields. It is possible that open boulder fields are the ideal microhabitat for *N. microlepidotus,* as they occur in the

largest numbers in the boulder fields (Melville and Swain, 1997a) but they are also able to exploit suboptimal microhabitats such as the heathlands.

Niveoscincus ocellatus

This study has confirmed that *Niveoscincus ocellatus* is a saxicolous species, occurring in open, rocky outcrops. It is the only species of *Niveoscincus* which is wholly saxicolous and occurs at low altitudes. There was no significant difference in microhabitat occupation between the two field sites. Lizards at Lake Augusta occupied a more open habitat than those at Orford. This is probably because the Orford field site is a dry sclerophyll woodland, while Lake Augusta is an open heathland with no canopy. Despite the huge differences between the two field sites these lizards still use the same microhabitat.

The Orford field site is woodland with shrubby undergrowth, extensive areas of litter, bare ground and outcrops of rock. Thus, there are many different microhabitats that *N. ocellatus* could occupy. Despite this the lizards use only a restricted and similar microhabitat to that recorded at Lake Augusta. This implies that they are actively selecting their microhabitat. There are a number of factors which could be the cause of this, including thermal requirements, morphological restrictions, or behavioural limitations. The influence of morphological and behavioural characteristics on microhabitat use will be discussed in Chapter 8. However, the thermal characteristics of the environment also have a pronounced impact on microhabitat occupation in ectotherms (Van Damme *et al.*, 1990). Microhabitat structure, particularly the presence of basking sites with different thermal characteristics, affects the time and precision required for temperature regulation. Thus, the thermal requirements of a lizard may influence the selection of microhabitats. Many studies have shown the importance of the thermal requirements of a lizard in microhabitat selection (eg. Schoener, 1970; Simon and Middendorf, 1976; Lee, 1980; Van Damme *et al.*, 1990). It is possible that the thermal requirements of *N. ocellatus* restrict it to the rocky outcrops at Orford and Lake Augusta.

Niveoscincus orocryptus (Mt Eliza)

Mt Eliza is the type locality for *N. orocryptus*, which was only described as a species in 1988 (Hutchinson *et al.*, 1988). It was described as a semi-arboreal species which spends much of its time moving through the shrubs and rocky outcrops in sub-alpine areas. It was also observed climbing the small eucalypt trees. This description agrees closely with the findings of the current study. *Niveoscincus orocryptus* were observed to bask both in the shrubs and rocks and were often seen basking at a height above 1 metre. The species was never found above the tree-line and appeared to be restricted to the sub-alpine woodland, which occurs in a small band at about 1000 m at Mt Eliza.

There was a distinct separation of the populations of *N. orocryptus* and *N. microlepidotus* at Mt Eliza. *Niveoscincus microlepidotus* occurred only above the tree-line, while *N. orocryptus* was only observed in the sub-alpine woodland. There did not appear to be any interactions at the boundary between the two species. This is probably not related to morphological restrictions. Much of the microhabitat that *N. orocryptus* occupies in the woodland is very similar to that in the open heathlands. Thus, it is possible that the separation of these two species is a result of different thermal requirements.

Many studies have reported that larger species are typically associated with more shaded areas and small ectotherms generally occupy warmer, more open microhabitats (see Scheibe, 1987; Marquet *et al.*, 1989). A canonical correlation analysis of temperate zone lizard communities revealed a significant relationship between lizard morphology and habitat use (Scheibe, 1987). Large bulky lizards were associated with extensive vegetation while smaller lizards were found in open desert or grasslands. Paulissen (1988) and Dent and Spellerberg (1987) reported that larger lizards occupied the more shaded areas in their study sites. They related the greater thermal inertia of these animals to the occupation of these less exposed microhabitats, where the risk of overheating was reduced. The spatial separation between *N. microlepidotus* and

N.orocryptus reported here did not reflect this, as *N. microlepidotus* is the larger species. This may be because Mt Eliza is in an alpine area. Larger lizards have lower surface area to volume ratios, so that the time required for warming is greater (Stevenson, 1985). Thus, these animals may require more open microhabitats in order to thermoregulate efficiently. It is also possible that the smaller lizard, *N. orocryptus*, occupies the more sheltered areas in order to avoid environmental extremes.

Niveoscincus orocryptus (Mt Hartz)

Niveoscincus orocryptus at the Mt Hartz field site occupy a significantly different microhabitat to the population at the Mt Eliza field site. The microhabitat occupied by *N. orocryptus* at Mt Hartz did not differ signifcantly from the microhabitat occupied by *N. microlepidotus* at the same field site. There were more individuals of *N. microlepidotus* in the boulder fields than *N. orocryptus* which is reflected by the lower scores on PC 1, indicating a more open habitat. The extensive overlap of the microhabitat use by *N. orocryptus* and *N. microlepidotus* is further confused by the similarity in appearance of the two species; identification had to be confirmed by capture. It has been reported that in the far south-west of Tasmania the populations of *N. microlepidotus/N. orocryptus* are morphologically indistinguishable and there are not even strong genetic differences (Hutchinson and Schwaner, 1991). Genetic relatedness was discussed in Chapter 3, where sequencing of the mitochondrial gene cytochrome *b* indicated that these species are distinguishable genetically.

Niveoscincus pretiosus

This study has shown that *Niveoscincus pretiosus* is a species which occupies forested areas, especially thickly vegetated habitats. *Niveoscincus pretiosus* was observed to move around on large fallen trees which create breaks in the canopy, providing large patches of sunlight for basking.

The two field sites used in this study are very different (see Chapter 2), yet the lizards occupy similar microhabitats. The Pirates Bay field site is a highly disturbed wet

sclerophyll forest. The land has been cleared and the current vegetation is regrowth. Lizards were recorded in greatest numbers moving around on large trees which had been bulldozed into piles in the forest. There were very few rocks at this field site and the lizards used logs exclusively as basking sites. The Clarence Lagoon field site, on the other hand, has large outcrops of rocks but *N. pretiosus* were rarely recorded using them as basking sites. The lizards at Clarence Lagoon consistently occupy the extensive areas of fallen trees.

Niveoscincus pretiosus has been described previously as a scansorial species adapted to living on fallen logs, trees or rock outcrops (Hutchinson *et al.*, 1989). This study found that it occurs in a range of habitats where there are trees or where rocks outcrop, using the elevated surfaces of fallen logs, the trunks and lower branches of trees, and less frequently rocks for basking sites. On some of the small islands inhabited by *N. pretiosus* trees are almost or totally absent and in these areas it is saxicolous (Hutchinson *et al.*, 1989). The current study indicates that on mainland Tasmania *N. pretiosus* is a forest-dwelling arboreal species. While searching for the two field sites the only locations where large numbers of *N. pretiosus* could be found were always damp, thickly forested areas. For example, at the Orford field site, which is mainly a dry sclerophyll area, *N. pretiosus* was only captured in the wet sclerophyll forest along the river edges.

Pseudemoia entrecasteauxii

This species is commonly known as the Tussock Skink. Rawlinson (1974), in his study of the biogeography of the Tasmanian reptiles noted that this species is restricted to tussocky vegetation, where it uses tussocks, low rocks and logs for basking. Greer (1982) described *P. entrecasteauxii* as a ground-dwelling species, which will ascend to low rocks and logs to bask. In the current study *P. entrecasteauxii* was only observed basking up to a height of 5 cm off the ground. The Hobart study site is a dry schlerophyll woodland and *P. entrecasteauxii* was found to occur in similar microhabitats to *N. metallicus* but in areas which had a higher percentage of ground

cover vegetation such as grass. Shine (1980), comparing a number of characteristics in gravid and non-gravid individuals of *Pseudemoia entrecasteauxii*, found that these lizards relied on speed and densely vegetated habitats to avoid predation. Similarly, the present study found this species to be very cryptic, often basking under cover of vegetation.

4.4.5 Microhabitat separation of the species

All species exhibited a non random selection of microhabitats and a preference for a particular set of environmental and structural factors. The selection of specific microhabitat characteristics by lizard communities has been reported in many studies (see Paulissen, 1988 for review). In the current study, microhabitat selection is strongly related to vegetation and substrate characteristics. The species differed significantly along PC axes 1 and 2 (Figure 4.2) which were associated with vegetation cover and height, substrate type and wetness. Other studies of lizard communities have found very similar factors to be involved in the selection of microhabitats. For example, Shenbrot *et al.* (1991) reported that the particle size of the substrate and the shelter available in the form of burrows or vegetation were the most important factors in determining the selection of microhabitats by some small desert dwelling lizards. Likewise, a number of studies of lizards dwelling in temperate climates have found that structural characteristics, such as vegetation type and substrate type, are of primary importance in microhabitat selection (Dent and Spellerberg, 1987; Paulissen, 1988; Patterson, 1992; Brown and Nelson, 1993). Vegetation height and density have been reported to be the primary factors in the selection of microhabitats by temperate lacertids and teiids (Dent and Spellerberg, 1987; Paulissen, 1988).

The importance of the presence of shrubs, grasses or rocks in determining the spatial distribution in skinks has been shown in a number of studies. The distribution of species of the genus *Leiolopisma*, which is closely related to *Niveoscincus*, appeared to be related primarily to the physical structure of the environment in the temperate grasslands of New Zealand (Patterson, 1992). Similarly, a study conducted in the

central highlands of Victoria on heliothermic skinks found that the distribution of species was related to the type of vegetation (Brown and Nelson, 1993). Larger species, for example *Eulamprus tympanum* and *Pseudemoia spenceri*, were more dependent on sites with open sunny patches than were smaller species such as *Niveoscincus coventryi*. This is similar to the findings of my study, in which the larger species (*N. ocellatus, N. greeni* and *N. microlepidotus*) selected microhabitats which were more open than the smaller species (*N. metallicus*, *N. coventryi* and *Pseudemoia entrecasteauxii*).

It is generally believed that the morphology of an organism relates to its ecology (Wainwright, 1991). Repeated patterns of similar morphological characteristics that correlate with specific habitat types, vegetation configurations, or other ecological attributes of species suggest a strong connection between morphology and ecology (Miles, 1994). However, the differences in microhabitat occupation which have been identified in *Niveoscincus* may be a result of a number of factors. These include competition between individuals, thermal requirements, or dietary differences (Toft, 1985).

Thermal biology and habitat use are interrelated because thermal microclimates vary spatially (Adolph, 1990). Habitat use by a particular lizard species reflects an overlap between the microhabitats that are thermally acceptable and those that are suited to its morphology and behavioural preferences (Adolph, 1990). The body temperature that a lizard is able to maintain has an important influence on many physiological processes and life history traits, including foraging success, digestion, gestation periods, growth rates, and reproductive potential (Adolph and Porter, 1993). For example, other studies have reported that the occupation of more open environments in alpine regions confers a number of advantages (Marquet *et al.*, 1989; Adolph and Porter, 1993). By selecting an open microhabitat a lizard has the opportunity to take advantage of more intense and longer periods of direct sunlight. *N. metallicus* and *N. microlepidotus* occupy separate microhabitats and have different thermal requirements within the same

sub-alpine environment, which is possibly a result of significantly different eccritic and critical temperatures (Melville and Swain, 1997a). Thus, it is possible that the differences in microhabitat use are influenced by the thermal requirements of the species.

Comparative studies have suggested that interference competition can be a cause of ecological differences among species (Talbot, 1979; Toft, 1985). The validity of evidence for the impact of interspecific competition on microhabitat utilisation, diets, and population dynamics of lizards is a contentious issue, and has been debated in many studies (Pacala and Roughgarden, 1985; Schoener and Gorman, 1968). Scheibe (1987) found that the clumping of lizard communities was a result of both ecological and morphological separation rather than competition. Aggressive interspecific interactions were recorded among a guild of *Leiolopisma* species, but in these small grassland skinks from New Zealand interspecific separation was unrelated to interference competition (Patterson, 1992). Rather, this separation was attributed to differences in microhabitat preferences and diet.

A possible example of interference competition was observed between *N. microlepidotus* and *N. greeni* at the Mt Pelion East field site, one of the very few areas where these two species co-exist. Microhabitat use by *N. microlepidotus* was very different at Mt Pelion East than at other field sites. Consequently, it was decided not to use this field site to study *N. microlepidotus*. *Niveoscincus greeni* from Mt Pelion East were included in the analysis because there was no significant difference between microhabitat use at this site and Ben Lomond. The microhabitat use by *N. greeni* at Mt Pelion East does not appear to be affected by the sympatry with *N. microlepidotus*. This was the only obvious occurrence of interference competition in this study.

Diet is often one of the most important resources partitioned in animal communities (Toft, 1985). Generally, the diet of a lizard species may be partitioned in two ways: prey type and foraging strategies. *Niveoscincus ocellatus* has been shown to be an

active forager that is opportunistic in prey selection (Wapstra, 1993), and *Niveoscincus* has been described collectively as a generalised insectivorous genus of active foragers (Brown, 1991). An extensive study of the feeding characteristics of a number of other small skinks endemic to south-eastern Australia demonstrated that most are opportunistic foragers (Brown, 1991). Thus it is unlikely that diet is of primary importance in the microhabitat separation of the species of *Niveoscincus*.

The morphological differences between the species, however, may be related to the selection of microhabitat by individuals. It has been suggested that there is a morphological phylogeny in *Niveoscincus* which includes the evolution of a scansorial habit (Hutchinson and Schwaner, 1991). Morphological differences between the species of *Niveoscinus* may mean that the less scansorial species are unable to utilise rocky outcrops or trees as mobility is detrimentally affected. At Clarence Lagoon *N. pretiosus* was seen climbing vertical tree trunks but this behaviour was never observed in *N. metallicus*. The arboreal species may be specialised morphologically for mobility within this habitat. This possibility is investigated further in the following chapters.

CHAPTER FIVE

LOCOMOTORY BEHAVIOUR IN THE FIELD

5.1 Introduction

Studies that integrate measurements of morphology, performance, behaviour and ecology are relatively rare (Garland and Losos, 1994). Behaviour is a very important factor in this paradigm, but has not been considered in many studies (Bauwens *et al.*, 1995). Animal species may have evolved specialised structures or morphologies which advantage a particular performance but without concurrent behavioural adaptation these are of little use. For example, gliding lizards possess increased surface areas to enhance gliding, but the most important factor in gliding is the outstretched posture, a behavioural adaptation, that arboreal lizards adopt (Garland and Losos, 1994).

The place of behaviour in the ecomorphological paradigm originally developed by Arnold (1983) was ambiguous and was not included as a distinct factor (Figure 5.1).

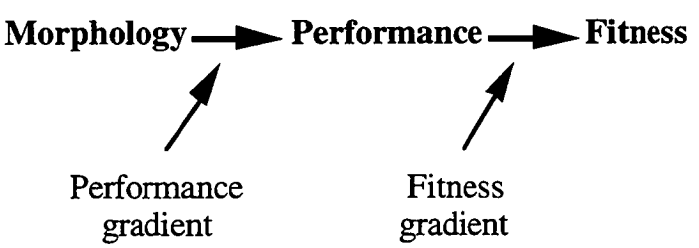


Figure 5.1 Simplified version of Arnold's (1983) original paradigm, taken from Garland and Losos (1994)

Subsequently, Emerson and Arnold (1989) included behaviour within the category of morphology. Garland and Losos (1994) offered an alternative categorisation (Figure 5.2), inserting behaviour between performance and fitness. This addition appears straightforward but the paradigm remained incomplete.

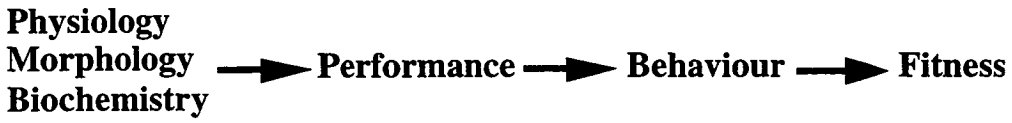


Figure 5.2 Expansion of Arnold's (1983) paradigm to include behaviour; taken from Garland and Losos (1994).

Garland and Losos (1994) added two more factors into Arnold's paradigm (1983): habitat and interspecific interactions (See Chapter 8). They pointed out that temperature, as a habitat characteristic, can affect both performance and behaviour. Temperature strongly affects a wide variety of physiological processes, ranging from enzyme reactions through to whole-animal processes, such as locomotion (Van Damme *et al.*, 1990). Consequently, at low body temperatures some lizards will change their behaviour in response to threat to a defensive posture rather than an escape tactic (Bennett, 1980; Arnold and Bennett, 1984; Van Damme *et al.*, 1990). Lizards at cold temperatures, when running ability is reduced, may display more aggressive behaviour, such as open mouth threats and biting (Hertz *et al.*, 1982; Mautz *et al.*, 1992).

Appendicular morphology and locomotory behaviour are correlated among flying (Findley and Wilson, 1982; Norberg, 1985), running (Hildebrand, 1974, 1985; Coombs 1978) and swimming (Webb and Blake, 1985) animals (see Losos, 1990a). Morphology and locomotory behaviour (eg. frequency of running and jumping) have been shown to have co-evolved (Losos, 1990a, b). A morphology-ecobehavioural comparison in the genus *Anolis* demonstrated that long-legged, long-tailed and heavy-bodied lizards jump and run more often, walk and move less often, and use lower perches than short-legged species. The habitat matrix model explains that this is a result of microhabitat differences (Moermond, 1979; Pounds, 1988). The model predicts that species will evolve morphologies necessary for the locomotory mode appropriate for a given microhabitat. Habitat-type was found to be important in determining locomotory behaviour, particularly jumping frequency and distance jumped, among 13 species of Jamaican and Puerto Rican anoles (Losos, 1990a). Similarly, in dense arboreal habitat,

saltation may be most efficient, whereas for lizards on isolated branches and trunks, running and crawling are more effective modes of movement (Losos, 1990a).

Locomotory behaviour has been shown to be a very important factor associated with morphology, microhabitat occupation and foraging success. Consequently, locomotor behaviour is a critical component of a lizard's life history (Pietruszka, 1986), but it has not been considered in many studies (Garland and Losos, 1994). For this reason I chose to examine the locomotory behaviour of the *Niveoscincus* species studied in the field and to compare the results with the ecomorph types established in Chapter 4. Do the three ecomorph types (saxicolous, arboreal and ground-dwelling) show significant differences in locomotory behaviour? This was quantified through multivariate analysis. The results from this analysis could then be used in further comparative phylogenetic analyses. Discriminant functions analyses were also used to examine the differences in behaviour between the species.

5.2 Materials and Methods

5.2.1 Field work

Behavioural focal samples were conducted following the procedures outlined by Moermond (1979) and Pounds (1988). Lizards were located by walking transects through each field site. These transects covered the range of available microhabitats at each site. Lizards were watched from a distance of 2-10 metres. Only undisturbed lizards were chosen for observation. Each lizard was watched for 10 minutes or until it disappeared. All movements were recorded as one of three behaviours: walk, climb, or jump. Walks were distinguished from climbs by the perch diameter and distance off the ground: if the subject was moving on a perch less than 50 cm in diameter and more than 20 cm above the ground it was considered a climb. Jump and climb data were included only from individuals that made more than two jumps. Only animals which performed at least two types of locomotor behaviours were included in the study; this effectively

excluded basking lizards or the escape behaviour of disturbed lizards. Observations were only conducted during good weather with limited cloud cover, as all *Niveoscincus* species spend the majority of their time inactive or basking during inclement weather. Jump and climb angles were measured with a 360° protractor with a line level attached to it, to allow accurate measurement of horizontal and vertical. A jump vertically down was recorded as an angle of 0°, while a leap vertically upwards was recorded as an angle of 180°. A climb which was horizontal had an angle of 0° and climbs up or down were measured as angles from the horizontal. This meant that lizards climbing upside-down had a climb angle greater than 90°. Movement distances were measured to the nearest centimetre; speed was estimated on a scale of 1 to 5, where 5 = maximum speed and 1 = very slow movement.

Ten variables of locomotory behaviour were recorded in the field:

1. jump angle (JA);
2. jump distance (JD);
3. climb angle (CA);
4. climb distance (CD);
5. estimated movement speed (ES);
6. walk distance (WD);
7. total movement distance (MD);
8. height off ground (HG);
9. perch diameter (PD); and
10. surface type (ST).

5.2.2 Statistical analysis

A principal components analysis (PCA) was carried out following the procedures used in Chapter 4. The data were not transformed prior to analysis as many of the values were zero and performing a log transformation would have resulted in the loss of valuable data. Rotation of data was not used since variables such as the walk distance and the total movement distance, which are in separate PCs, are to some extent

dependent upon each other. I believe the results of this analysis were able to be interpreted adequately without rotation.

The mean scores of each PC axis were calculated for all the *Niveoscincus* populations as well as the *Pseudemoia entrecasteauxii* population. These values could then be used in the Independent Contrasts analysis in Chapter 8 as a measurement of microhabitat occupation.

Subsequently, a direct discriminant function analysis (MGLH procedure of SYSTAT, Wilkinson *et al.*, 1992) was performed on the PC axes of each species. Univariate and multivariate outliers were identified for each species and those that were significant were eliminated before the analysis.

5.3 Results

5.3.1 Locomotory behaviour

A consistent and obvious relationship existed between the three locomotory variables measured. Those species which predominantly walk, such as *N. coventryi* and *P. entrecasteauxii*, tend not to jump and climb very little (Table 5.1). It was found that the species formed four distinct behavioural groups: saxicolous (*N. greeni* and *N. ocellatus*); heath/rock-dwelling (*N. microlepidotus* and *N. orocryptus* (Mt Hartz)); arboreal (*N. pretiosus* and *N. orocryptus* (Mt Eliza)); and ground-dwelling (*N. metallicus, N. coventryi* and *P. entrecasteauxii*). Consequently, unlike in Chapter 4, there were four ecomorphological groups included in the analyses in this chapter.

The mean distance walked by lizards in a 10 minute observation period varied greatly, from a minimum of 11.5 cm by *N. greeni* (Ben Lomond) to a maximum of 65.6 cm by *P. entrecasteauxii* (Table 5.1). The species that walked the furthest were the ground-dwelling species, such as *N. coventryi, N. metallicus* and *P. entrecasteauxii*. An analysis

of variance indicated a significant difference between the walk distance of the ecomorph types ($F_{3,1002}$ = 1258.25, $p<0.001$). A Fisher's LSD post hoc test showed no significant difference in the distance walked by the saxicolous (*N. greeni, N. orocryptus* (Mt Hartz), *N. ocellatus* and *N. microlepidotus*) and arboreal (*N. pretiosus* and *N. orocryptus* (Mt Eliza)) species. However, there was a significant difference between the ground-dwelling (*N. metallicus, N. coventryi* and *P. entrecasteauxii*) and all the other species ($p<0.001$).

The distance climbed by lizards also varied greatly. *Pseudemoia entrecasteauxii* was never observed to climb a measurable distance, while *N. orocryptus* (Mt Eliza) and *N. pretiosus* (Clarence Lagoon) both averaged climbs of 45.9 cm in a 10 minute period (Table 5.1). The lizards that climbed the furthest distance also climbed at the largest angles. *Niveoscincus pretiosus* (Clarence Lagoon) climbed at a mean angle of 58°. Not surprisingly, the arboreal species climbed the furthest distances. An analysis of variance indicated a significant difference in climb distance between the ecomorph types ($F_{3,1002}$ = 183.34, $p<0.001$). A Fisher's LSD post hoc test showed that the difference was significant between all pairs of ecomorphs ($p<0.05$).

A number of the species were never observed to jump during the study. These were *N. coventryi, N. metallicus, N. pretiosus* and *P. entrecasteauxii* (Table 5.1). Consequently, there was a significant difference between the jump distance recorded for the various ecomorphs ($F_{3,1002}$ = 243.89, $p<0.001$) and a Fisher's LSD post hoc test showed a significant difference between all pairs of ecomorphs ($p<0.05$). The species that jumped the furthest (*N. greeni* from Ben Lomond) also jumped at the largest angle. The two populations of *N. greeni* differed significantly in jump distance ($F_{1,155}$ = 53.72, $p<0.001$).

Table 5.1 Locomotory behaviour recorded for each population of *Niveoscincus* and *Pseudemoia entrecasteauxii* (values are means ± standard error)

	n	Walk distance (cm)	Climb dist. (cm)	Climb angle (°)	Jump distance (cm)	Jump angle (°)	Perch height (cm)	Total dist. (cm)
N. coventryi (Mt St Leonards)	72	55.1 ± 8.84	1.9 ± 0.21	4.3 ± 2.31	0.0	0.0	1.1 ± 0.53	38.4 ± 3.64
N. greeni (Ben Lomond)	82	11.5 ± 2.02	15.1 ± 2.07	20.2 ± 1.72	39.8 ± 1.43	39.4 ± 2.60	98.6 ± 7.63	84.0 ± 5.60
N greeni (Mt Pelion East)	75	20.3 ± 1.22	23.9 ± 1.71	33.9 ± 1.79	22.18 ± 2.75	32.6 ± 3.33	91.2 ± 5.34	89.7 ± 4.58
N. metallicus (Orford)	78	35.4 ± 8.41	2.6 ± 1.25	6.7 ± 5.14	0.0	0.0	4.1 ± 1.15	71.4 ± 3.19
N. metallicus (Clarence Lagoon)	76	50.4 ± 5.47	4.1 ± 1.41	10.3 ± 6.48	0.0	0.0	14.2 ± 1.88	75.2 ± 5.36
N. microlepidotus (Mt Hartz)	83	20.1 ± 2.16	19.2 ± 1.82	25.0 ± 2.30	12.5 ± 1.32	25.1 ± 1.84	66.4 ± 2.94	105.1 ± 2.16
N. microlepidotus (Mt Wellington)	81	28.4 ± 1.92	24.0 ± 1.37	24.3 ± 1.63	14.4 ± 0.93	25.4 ± 1.11	90.4 ± 7.45	122.0 ± 7.89
N. ocellatus (Lake Augusta)	79	19.2 ± 1.61	14.9 ± 1.45	16.4 ± 1.94	22.5 ± 2.15	34.6 ± 2.68	99.8 ± 6.76	75.5 ± 5.69
N. ocellatus (Orford)	81	20.9 ± 1.67	12.5 ± 1.08	16.2 ± 1.44	23.3 ± 1.97	38.1 ± 2.72	52.8 ± 2.29	80.5 ± 5.78
N. orocryptus (Mt Eliza)	84	13.6 ± 1.35	49.5 ± 6.72	43.1 ± 5.32	6.1 ± 1.35	14.0 ± 1.81	138.6 ± 10.84	81.5 ± 9.92
N. orocryptus (Mt Hartz)	82	19.5 ± 2.03	22.2 ± 0.82	22.9 ± 2.28	14.4 ± 0.96	25.7 ± 1.21	73.1 ± 3.83	102.1 ± 6.65
N. pretiosus (Clarence Lagoon)	80	15.33 ± 2.09	49.5 ± 3.09	58.0 ± 5.64	0.0	0.0	79.8 ± 9.05	91.3 ± 8.62
N. pretiosus (Pirates Bay)	79	14.9 ± 3.36	38.9 ± 4.74	40.9 ± 5.25	0.0	0.0	101.6 ± 10.51	82.2 ± 8.81
P. entrecasteauxii (Hobart)	74	65.6 ± 3.18	0.0	0.0	0.0	0.0	0.0	42.0 ± 6.74

The two heath and rock dwelling species (*N. microlepidotus* and *N. orocryptus* (Mt Hartz)) moved the greatest distance in a ten minute period (Table 5.1). An analysis of variance indicated a significant difference between the total distance moved by the four ecomorph types ($F_{3,1002} = 97.61$, $p<0.001$). Fisher's LSD post hoc test indicated that differences between the saxicolous (*N. greeni, N. orocryptus* (Mt Hartz), *N. ocellatus* and *N. microlepidotus*) and arboreal (*N. pretiosus* and *N. orocryptus* (Mt Eliza)) species were not significant, but there was a significant difference between the ground-dwelling species (*N. metallicus, N. coventryi* and *P. entrecasteauxii*) and all other ecomorphs ($p<0.05$).

5.3.2 Multivariate analysis of locomotory behaviour

The analysis described below was first performed separately on both sexes of each species. However, since no significant differences were found between sexes, the data for each species were then pooled.

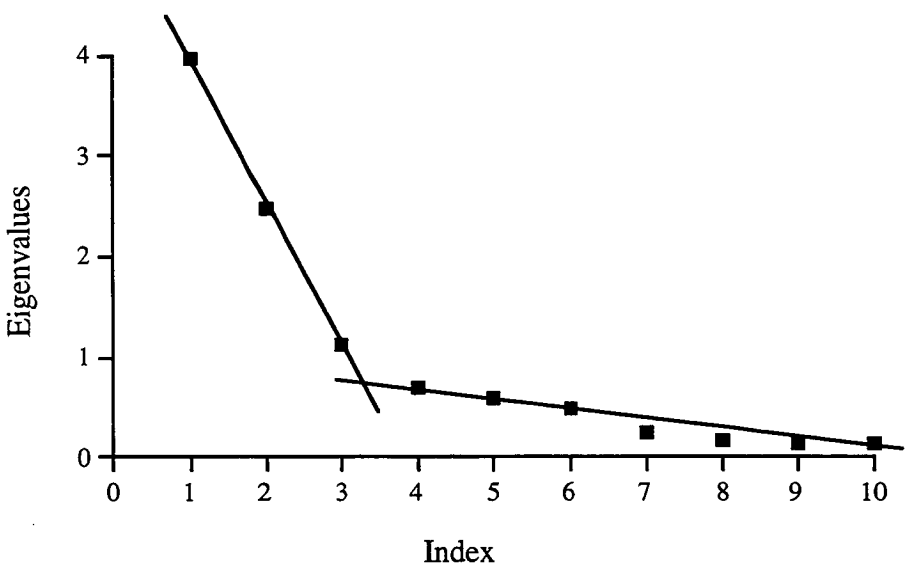


Figure 5.3 Scree plot of eigenvalues derived from principal components analysis.

The first three PCA factors accounted for 75.68% of the variance of the raw data (Table 5.2). The number of factors used in the analysis was determined using a scree

test (Figure 5.3), where the change in slope indicated the number of factors which should be used. The first PC yielded a strong positive correlation between the estimated movement speed (ES), jump angle (JA) and jump distance (JD). A strong negative correlation was revealed between climb distance (CD), climb angle (CA), walk distance (WD) and surface type (ST) and those factors mentioned above (Table 5.2). Thus, the PC 1 axis described a locomotory gradient in which high PC scores denoted jumping behaviour and rapid movement and low PC scores denoted climbing behaviour with slow movement. The second PC axis showed strong positive correlation with height off the ground (HG) and a negative correlation with perch diameter (PD) (Table 5.2). This represents a gradient of arboreality in which low PC 2 scores denoted movement close to the ground and high scores denoted movement above the ground on small perches. The third PC axis revealed a strong negative correlation with the distance a lizard moved (MD). High PC 3 scores represented little movement and low PC 3 scores indicated long distances moved.

PC1 was accepted for the independent contrasts analysis (Chapter 8) because it accounted for the largest percentage of the variance of the raw data (Table 5.2) and represented the largest section of locomotory behaviour. PC2 and PC3 represented only the height off the ground and the movement distance respectively.

A direct discriminant function analysis was performed using the three PC axes as predictors of the occupation of basking sites by members of each species. Of the 1110 lizards recorded, four were identified as outliers and subsequently removed from the analysis. Two of the statistical outliers were *N. pretiosus* that had been observed walking across open ground. One other outlier was a *N. metallicus* recorded leaping off a small rock; it was unclear if this was escape behaviour or not. The remaining outlier was a *N. metallicus* that was observed climbing a large tree trunk vertically, 2 metres above the ground. Assumptions of linearity and normality were not violated for the remaining 1106 animals.

Table 5.2 Correlations of original environmental variables with the first three PC scores for *Niveoscincus* species and *Pseudemoia entrecasteauxii.*

	PC 1		PC 2		PC 3
Correlations with PCs	CD -0.690	ES 0.833	PD -0.803	HG 0.718	MD -0.642
	CA -0.741	JD 0.628			
	ST -.857	JA 0.605			
	WD -.856				
Percent of variance	39.75		24.7		11.23
Group	n	Score (mean ± se)	Score (mean ± se)		Score (mean ± se)
N. coventryi (Mt St Leonards)	72	-0.07 ± 0.004	-1.64 ± 0.003		0.52± 0.002
N. greeni (Ben Lomond)	82	1.31 ± 0.036	1.15 ± 0.061		0.08 ± 0.118
N greeni (Mt Pelion East)	75	0.99 ± 0.056	0.63 ± 0.097		0.04 ± 0.157
N. metallicus (Orford)	78	0.02 ± 0.006	-1.46 ± 0.057		0.39 ± 0.040
N. metallicus (Clarence Lagoon)	76	-0.01 ± 0.022	-0.98 ± 0.079		0.12 ± 0.049
N. microlepidotus (Mt Hartz)	83	-0.01 ± 0.055	0.13 ± 0.085		-0.31 ± 0.113
N. microlepidotus (Mt Wellington)	81	0.10 ± 0.042	0.17 ± 0.063		-0.95 ± 0.111
N. ocellatus (Lake Augusta)	79	0.77 ± 0.054	0.27 ± 0.092		-0.10 ± 0.153
N. ocellatus (Orford)	81	0.89 ± 0.043	0.22 ± 0.074		-0.03 ± 0.137
N. orocryptus (Mt Eliza)	84	-1.71 ± 0.127	1.00 ± 0.112		0.03 ± 0.211
N. orocryptus (Mt Hartz)	82	0.04 ± 0.038	-0.03 ± 0.074		-0.61 ± 0.102
N. pretiosus (Clarence Lagoon)	80	-1.58 ± 0.088	0.47 ± 0.064		0.05 ± 0.207
N. pretiosus (Pirates Bay)	79	-1.40 ± 0.073	0.36 ± 0.098		-0.27 ± 0.152
P. entrecasteauxii (Hobart)	74	-0.06 ± 0.001	-1.65 ± 0.000		0.52 ± 0.002

A discriminant function analysis showed that there were interspecific differences in PC scores on both PC 1 and 2 (Table 5.2). On PC 1 the highest mean score was for *N.*

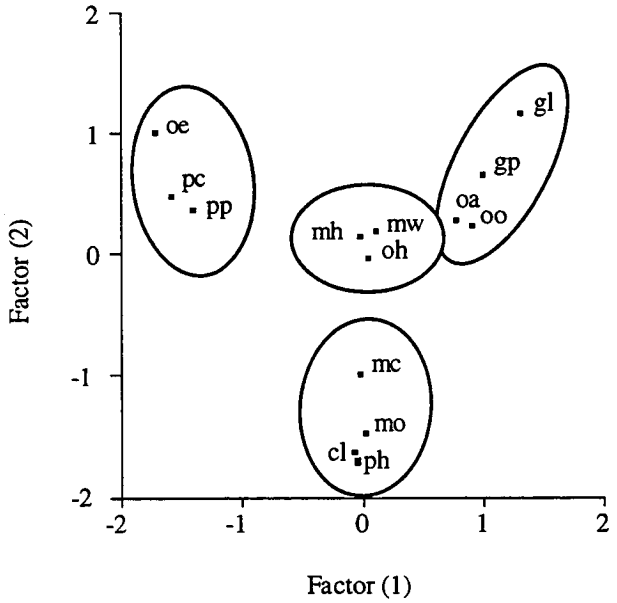
greeni (Ben Lomond), indicating that this species spent a large amount of time jumping. The lowest mean score was for *N. orocryptus* (Mt Eliza), which demonstrated that this species predominantly climbed through its environment.

There were significant differences between the species on PC 1 ($F_{8,1097}$ = 729.17, P<0.001). A Fisher's LSD post hoc test revealed that *N. orocryptus* (Mt Hartz), *N. microlepidotus, N. metallicus, N. coventryi* and *P. entrecasteauxii* did not differ significantly from each other on PC1. On PC 2 the highest mean score was shown by *N. greeni* (Ben Lomond), while *P. entrecasteauxii* had the lowest mean score (Table 5.2, Figure 5.4). There were significant differences between species on PC 2 ($F_{8,1097}$ = 340, P<0.001). However, a post hoc test indicated that there were no significant differences between: *N. coventryi* and *P. entrecasteauxii*, *N. orocryptus* (Mt Eliza) and *N. greeni*, or between *N. microlepidotus* and *N. orocryptus* (Mt Hartz).

The populations of *N. pretiosus* ($F_{1,157}$ = 5.21, p = 0.024), *N. microlepidotus* ($F_{1,162}$ = 5.27, p = 0.023), *N. ocellatus* ($F_{1,158}$ = 24.43, p<0.001) and *N. greeni* ($F_{1,155}$ = 13.89, P<0.001) showed significant intraspecific differences on PC 1. On PC 2 there were significant differences between the populations of *N. metallicus* ($F_{1,152}$ = 65.68, P<0.001) and *N. greeni* ($F_{1,155}$ = 28.44, P<0.001), but there were no significant differences between the populations of *N. microlepidotus, N. ocellatus* and *N. pretiosus.* On PC 3 there were significant intraspecific differences between the populations of: *N. metallicus* ($F_{1,152}$ = 53.90, P<0.001), *N. greeni* ($F_{1,155}$ = 14.31, p<0.001), *N. microlepidotus* ($F_{1,162}$ = 46.02, p< 0.001), *N. ocellatus* ($F_{1,158}$ = 5.63, p = 0.019) and *N. pretiosus* ($F_{1,157}$ = 7.254, p = 0.008).

Some of the species which were recorded at the same field sites showed significantly different scores along the PC axes (Figure 5.4). For example, *N. metallicus* and *N. ocellatus* at the Orford field site exhibited significantly different locomotory behaviour as shown by PC1 ($F_{1,157}$ = 491.63, P<0.001), PC 2 ($F_{1,157}$ = 467.68, P<0.001) and PC 3 ($F_{1,157}$ = 13.48, P<0.001). A similar situation occured at Clarence Lagoon with *N.*

metallicus and *N. pretiosus* PC 1 ($F_{1,154}$ = 99.98, P<0.001) and PC 2 ($F_{1,154}$ = 79.48, P<0.001). However, *N. microlepidotus* and *N. orocryptus* at Mt Hartz show no significant differences on PC1 ($F_{1,163}$ = 0.136, P = 0.233).



cl - *N. coventryi* (Mt St Leonards)
gl - *N. greeni* (Ben Lomond)
gp - *N. greeni* (Mt Pelion East)
mc - *N. metallicus* (Clarence Lagoon)
mo - *N. metallicus* (Orford)
mh - *N. microlepidotus* (Mt Hartz)
mw - *N. microlepidotus* (Mt Wellington)
oa - *N. ocellatus* (Lake Augusta)
oo - *N. ocellatus* (Orford)
oe - *N. orocryptus* (Mt Eliza)
oh - *N. orocryptus* (Mt Hartz)
pc - *N. pretiosus* (Clarence Lagoon)
pp - *N. pretiosus* (Pirates Bay)
ph - *P. entracasteauxii* (Hobart)

Figure 5.4 The first two principal components axes of the *Niveoscincus* species and *Pseudemoia entrecasteauxii.*

The species were grouped together according to ecomorph type (ground-dwelling, arboreal, heath/rock-dwelling or saxicolous) for further analysis. *Niveoscincus greeni* and *N. ocellatus* were classed as saxicolous species. *N. microlepidotus* and *N. orocryptus* (Mt Hartz) formed the heath/rock-dwelling species. *Niveoscincus metallicus, N. coventryi* and *Pseudemoia entrecasteauxii* were grouped together as ground-dwelling lizards. *Niveoscincus pretiosus* and *N. orocryptus* (Mt Eliza) formed the arboreal group. A direct discriminant function analysis was performed on these four groupings, using the first two PC axes as predictors of locomotory behaviour (Figure 5.4).

The discriminant function analysis revealed that the PC scores for the ecomorph types differed on both PC 1 ($F_{3,1103} = 1391.05$, $P<0.001$) and PC 2 ($F_{3,1103} = 974.44$, $P<0.001$). A Fisher's LSD post hoc test applied to PC1 showed that the mean scores for all the ecomorphs differed significantly from each other on each PC axis ($p<0.05$).

5.4 Discussion

5.4.1 Locomotory behaviour in *Niveoscincus*

This is the first study to quantify locomotory behaviour in *Niveoscincus*. Previous studies consist only of brief descriptions of how *Niveoscincus* species move through their environment. Hutchinson and Schwaner (1991) have suggested that there are a number of lineages of locomotory form in *Niveoscincus*, consisting of two ground-dwelling species (*N. metallicus* and *N. coventryi*), the arboreal species *N. pretiosus*, the saxicolous species *N. ocellatus* and the three alpine species (*N. microlepidotus, N. greeni* and *N. orocryptus*). Hutchinson and Schwaner (1991) consider *N. ocellatus* and the alpine species to be two separate lineages of scansoriality and *N. pretiosus* to be a third lineage of scansoriality.

The current study (Chapter 3) has shown that the phylogeny of *Niveoscincus* does not indicate that *N. ocellatus* is a separate lineage of scansoriality. However, it does appear that four separate types of locomotory behaviour can be recognised in *Niveoscincus*. These are the ground-dwelling species (*N. metallicus* and *N. coventryi*), the arboreal species (*N. pretiosus* and *N. orocryptus* (Mt Eliza)), the saxicolous species (*N. greeni* and *N. ocellatus*) and the heath/rock-dwelling species (*N. orocryptus* (Mt Hartz) and *N microlepidotus*). Each of these groups formed distinct clusters in the principle components analysis (Figure 5.2).

Niveoscincus metallicus and *N. coventryi* are primarily ground-dwelling and lack derived character states associated with some degree of scansoriality (Hutchinson and Schwaner, 1991). They have relatively short limbs, large midbody scales, and relatively large litters which are consistent features of ground-dwelling lizards (Rawlinson, 1974, 1975; Hutchinson *et al.*, 1990). The current study has confirmed and quantified the ground-dwelling behaviour of *N. metallicus* and *N. coventryi*. They are both species which walk through their environment remaining close to the ground. Similar behaviour was recorded for *Pseudemoia entrecasteauxii*, and this species was indistinguishable from *N. coventryi* on both PC 1 and 2.

Niveoscincus metallicus is more scansorial than *N. coventryi* and *Pseudemoia entrecasteauxii*. It was observed to often climb onto rocks and logs to bask. Rawlinson (1975) and Greer (1983) report that *N. metallicus* uses fallen logs, the trunks and lower limbs of trees and rock surfaces for basking, but spends most of its time at ground level. *Niveoscincus coventryi* and *P. entrecasteauxii*, on the other hand, demonstrate almost no scansorial behaviour. These species, especially *N. coventryi*, stay on the ground and climb very rarely. This is supported by the findings of Webb (1985), who reported that *N. coventryi* is a ground-dwelling species that will utilise only small pieces of wood on the ground, litter and ground-cover as basking sites.

It has been suggested that *N. pretiosus* represents a second lineage of locomotory behaviour in *Niveoscincus* (Hutchinson and Schwaner, 1991). This species has the smallest body size within the genus and has been described as the most arboreal (Hutchinson and Schwaner, 1991). It is very agile and uses elevated surfaces for movement (Rawlinson, 1975). However, my study has found that *N. orocryptus* at Mt Eliza is also highly arboreal. Both *N. pretiosus* and *N. orocryptus* (Mt Eliza) were found to predominantly climb through their environment. *Niveoscincus orocryptus* (Mt Eliza) occasionally jumped, but *N. pretiosus* was never seen jumping. This may be a result of the different microhabitats inhabited by the two species. Individuals of *N. orocryptus* at Mt Eliza spent a higher percentage of their time on rocks than did

those of *N. pretiosus*, and were observed to jump off these rocks occasionally. *Niveoscincus pretiosus* has been seen moving around on rocky beaches in far southwestern Tasmania (pers. obs.), but even on this rocky surface I have never seen them jump. They invariably climb and run through their environment.

Niveoscincus ocellatus is the most morphologically distinct species of *Niveoscincus* and is primarily a rock dweller, believed to represent a distinct lineage of scansoriality by Hutchinson and Schwaner (1991). However, the locomotory behaviour of this species did not differ significantly from that of *N. greeni* on PC 1. Both species were frequently observed climbing over the rocky substrate they inhabit but they were also seen to jump from one rock to another. They are both highly mobile and move rapidly through their environment by jumping and climbing over the rock surfaces. Most of the jumps recorded consisted of the lizards jumping from the top of one rock to a lower one. Jumping has not been reported before in *N. ocellatus* but has been observed previously in *N. greeni*. Greer (1983) observed that *N. greeni*, when alarmed, would usually flee into crevices between rocks but a few jumped into an adjacent creek. He described them dashing after passing insects and even observed one juvenile foraging for a distance of 25 m, during which it occasionally jumped into the water to get from one rock to another.

Interestingly, the locomotory behaviour of *N. greeni* differed significantly at the two field sites. The lizards at Mt Pelion East jump shorter distances and climbed further than those at Ben Lomond. This is possibly because of differences in the microhabitat between the two field sites. The rocks at Mt Pelion East are smaller and flatter than those at Ben Lomond, because rocks falling from higher up the slope have fragmented, forming rocky stacks in many places (see Chapter 2). The boulders at Ben Lomond are large and separated by deep crevices. Consequently, the microhabitat at Mt Pelion East is more continuous than at Ben Lomond, where the boulder fields form a more discontinuous habitat. Thus, it may be more efficient to move around by climbing at Mt Pelion East and by jumping at Ben Lomond.

The other two exclusively alpine species, *N. microlepidotus* and *N. orocryptus* (Mt Hartz), make up the fourth group of locomotory behaviour identified here. These two species, along with *N. greeni*, have been reported as exhibiting the greatest degree of specialisation in ecology, morphology and behaviour within *Niveoscincus* (Hutchinson, Schwaner and Medlock, 1988). However, *N. greeni* was significantly different from *N. microlepidotus* and *N. orocryptus* (Mt Hartz) in locomotory behaviour on both PC 1 and 2 (Figure 5.4).

Niveoscincus microlepidotus has been described as an agile and scansorial species, adapted to living on fallen logs, trees or rock outcrops (Hutchinson *et al.*, 1989). My study has shown that this species and *N. orocryptus* (Mt Hartz) are the only species of *Niveoscincus* which walk, climb, and jump to similar degrees. They were also found on a range of perch types and heights. *Niveoscincus microlepidotus* and *N. orocryptus* (Mt Hartz) appear to be generalised alpine species, able to move through their environment in a number of ways and can successfully utilise a number of microhabitats, including rocks, heath and open woodlands (Chapter 4). They contrast markedly with *N. greeni* which appears to be a saxicolous alpine species. *Niveoscincus microlepidotus* and *N. orocryptus* (Mt Hartz) are also the species that covered the greatest total distance within a standard observation period. They averaged 1.0 to 1.5 metres within a 10 minute period and some were observed to move much further. In contrast the cryptic ground-dwelling species such as *N. coventryi* and *N. entrecasteauxii* were observed to move only short distances.

5.4.2 Locomotory behaviour in the study of ecomorphology

Significant differences in locomotory behaviour allows four ecomorph types to be identified (ground-dwelling, arboreal heath/rock-dwelling and saxicolous) within *Niveoscincus*. It is possible to identify two ecomorph types within the original saxicolous group identified in Chapter 4. *Niveoscincus ocellatus* and *N. greeni* are

significantly different from the heath/rock-dwelling species *N. microlepidotus* and *N. orocryptus* (Mt Hartz) when locomotory behaviour is taken into account.

Implicit in the concept of ecomorphs (Rand and Williams, 1969; Williams, 1972, 1983) is the assumption that morphology and locomotory behaviour have evolved synchronously. Losos (1990) has argued that the locomotory behaviour of a species is related to its morphology: the clustering pattern of locomotory behaviour in the genus *Anolis* is the same as the clustering of morphology. However, differences in locomotory behaviour have more often been attributed to other factors, such as microhabitat (Moermond, 1986) or foraging mode (Losos, 1990). For example, Moermond (1986) found that two species of *Anolis* which occupied a similar portion of habitat used their habitat in different ways. *Anolis aenus* jumped in only 27% of the observed movements, compared to 41% for *A. richardi*. Sit-and-wait anoles search through their habitat by changing their location with some frequency. *Anolis aenus* was more of an active searcher than *A. richardi*, moving frequently along perches, especially when on large tree trunks. The differences in leg morphology in these species also corresponded to differences in movement and hunting behaviour (Moermond, 1986).

The habitat matrix model predicts that as members of the same ecomorph category occupy similar microhabitats they should be similar in behaviour (Moermond, 1986). Pounds (1988) demonstrated that behaviour varies intraspecifically in a predictable manner as a consequence of microhabitat structure. Moermond (1979) attributed differences in the rate of movement among ecomorphs to differences in microhabitat. He contended that anoles on trunks can scan an area for prey more quickly and therefore move more often than anoles in more cluttered habitats, such as grasses or bushes.

I have argued that the difference in locomotory behaviour exhibited by *N. greeni* at the two field sites examined may be a consequence of microhabitat differences. Losos (1990) observed a similar situation in two anoles (*Anolis evermanni* and *A. gundlachi*) which both inhabited trunk and boulder microhabitats. The boulders represented a

discontinuous habitat matrix and to get from one boulder to the next lizards could jump or run down one boulder and across to the next. In contrast, the tree trunks represented a continuous surface which did not require jumping. As in *Niveoscincus greeni*, both species of anole jumped more in the discontinuous microhabitat.

It has frequently been reported that both locomotory mode and habitat may affect social behaviour (Losos, 1990). When the movement rates of anoles were classed as either rapid or slow, display frequencies of these animals were correlated with rapid movement (Losos, 1990). *Anolis valencienni* is an active forager, which is unusual for anoles (Losos, 1990). Its rate of movement was not exceptional, but the amount of time the species spent moving was unusually long. *Anolis valencienni* moves slowly, sometimes covering distances greater than 5 metres along trunks and branches without stopping. This species was less territorial, had a low display rate, which was used as a measure of social behaviour, and had cryptic colouring. This was thought to relate to the higher predation risk associated with active foraging. Other anoles move in short, rapid bursts, interspersed with relatively long periods of inactivity and are often aggressive, territorial lizards (Losos, 1990).

Social behaviour in *Niveoscincus* has not been studied but differences in the levels of aggression shown by the species are apparent in the laboratory. Individuals of the alpine species (*N. orocryptus* (Mt Hartz), *N. greeni* and *N. microlepidotus*) often interacted aggressively towards each other and could badly injure each other through head and tail biting. Interactions between individuals of these species in the field usually consisted of larger lizards chasing smaller lizards off basking sites. Interactions of this nature were also observed on a number of occasions between individuals of *N. pretiosus*. Aggressive behaviour between individuals of other species was not observed. Thus, the more aggressive species in *Niveoscincus* are the highly mobile and widely moving species.

The differences in social behaviour between species of *Niveoscincus* may be related to microhabitat. Moermond (1979) suggested that perch characteristics within microhabitats may be important for predator avoidance, male advertisement, and

territorial patrolling. Thus, it is possibly that the alpine species, which occupy open habitats, are more aggressive because they are able to view more of their surroundings. Ideal basking sites, which provide thermal or possibly even male advertisement opportunities, may be a limited resource in the alpine environment. Thus, the defence of basking sites may have a selective advantage. Consequently, social behaviour and microhabitat occupation in *Niveoscincus* may have evolved in synchrony.

The evolution of specific anti-predator tactics will often depend on the existence or the coevolution of other aspects of an animal's behaviour or morphology (Bauwens and Thoen, 1981). Arnold (1994) suggests that sit-and-wait foraging is a common technique for lizards in open habitats where many potential prey items tend to be infrequent and mobile, and that this has coevolved with other behaviours in some species. For example, surface-dwelling sand lizards dive rapidly into loose sand when evading predators, a behaviour which has different origins in different lizard groups. It is believed to have evolved directly from predator evasion in sandy habitats in the lacertid genus *Meroles* (Arnold, 1995). However, the skink *Mabuya acutilabris* holds its body straight when diving, a posture that probably originated in the context of concealment at the end of activity (Arnold, 1995). Thus, behaviour may not be solely a result of the microhabitat in which a lizard lives.

The effectiveness of crypsis often depends largely on the ability of an animal to remain motionless (Bauwens and Thoen, 1981). It might be expected that an animal that is cryptic to its predators, both in morphology and behaviour, will also be cryptic to its prey. Thus, the best way for a cryptic animal to gather food is to be a sit-and-wait predator (Bauwens and Thoen, 1981). An animal that does not strongly rely on remaining motionless to avoid predation is not restricted in its foraging habits and may actively search out its prey. The more cryptic species of *Niveoscincus*, such as *N. coventryi*, move significantly less than those which inhabit open areas, such as *N. microlepidotus*. It might be expected, therefore, that the more cryptic species would be sit-and-wait predators. However, a study of the south-eastern Australian skinks reported that they are all opportunistic and widely foraging generalists (Brown, 1991)

and *N. ocellatus* has recently been shown to fit this description (Wapstra and Swain, 1996). Traditionally, lizards have been classified as either "sit-and-wait" or "active" foragers (Pianka 1966), but these represent the extremes of a continuum (Pietruszka, 1986). Thus, it is possible that the species of *Niveoscincus* present a gradient of foraging modes, ranging from widely foraging species, such as *N. microlepidotus,* through to foragers that are more restricted in the distance over which they move, such as *N. coventryi.*

A variety of attributes has been found to distinguish the two foraging modes among terrestrial lizards. Sit-and-wait foragers tend to be stocky, have short tails, and carry relatively large clutches, whereas active foragers are often slender, with long tails and relatively small clutches (Huey and Pianka, 1981; Vitt and Price, 1982; Perry *et al.*, 1990). The two foraging modes tend to differ in sprint speed and endurance in a predictable manner (Garland and Losos, 1994). Thus, active foragers have greater endurance, but sit-and-wait foragers often have a greater sprinting ability (Huey *et al.*, 1984). *Niveoscincus* appears to follow this trend and this will be discussed further in the following chapters.

CHAPTER SIX

PERFORMANCE ABILITIES

6.1 Introduction

Relationships between morphology and physiology or between behaviour and ecology have been widely documented (see Garland and Losos, 1994). Early ecomorphological analyses tended to examine correlations between morphology and ecology (Miles, 1994). These studies provide evidence that most organisms are to some extent "adapted" to their current environment. Quantifying how well adapted an organism is to its environment may be very difficult, many studies in ecomorphology have ignored the crucial intermediate step of organismal performance when trying to link ecology and morphology (Garland and Losos, 1994). Maximal performance abilities, when considered in conjunction with behaviour in the field, can provide the link when examining the mechanistic basis for the link between morphology and ecology.

Studies of ecological morphology implicitly concern fitness and adaptation (Garland and Losos, 1994). The incorporation of locomotion into these studies is a particularly productive avenue for investigation of the underlying mechanism of trade-offs in evolutionary adaptation (Losos *et al.*, 1993), since variation in locomotory performance may affect an organism's ability to exploit specific ecological opportunities (Huey and Stevenson, 1979). For example, most behaviour in lizards, such as escape or feeding behaviour, involves some form of locomotion. Consequently, locomotor capacities are potentially relevant to organismal fitness (Arnold, 1983).

Physiological ecologists and evolutionary biologists have recently focused on studies of whole organism performance capability to understand whether and how organisms are adapted to their environment (eg. Arnold, 1983; Huey and Bennett, 1987; Garland and Losos, 1994; Losos and Irschick, 1996). Implicit in this approach is the assumption that laboratory measures of performance are relevant to the behaviour of organisms in

nature. The maximum sprinting capabilities of lizards and snakes are affected by a wide variety of factors, including body temperature, gravidity, tail loss and exhaustion (Vitt, 1983; Garland and Losos, 1994; Bauwens *et al.*, 1995). In turn, field studies have documented that when locomotor ability is impaired, individuals alter their behaviour by fleeing at a greater approach distance as a predator approaches, exhibiting more cryptic behaviour or aggressively defending themselves (Hertz *et al.*, 1982; Mautz *et al.*, 1992).

Arnold (1983) described performance as a measure of an ecologically relevant activity, such as running speed. A variety of such measures of performance have been quantified in lizards and snakes, including sprint speed (eg. Huey, 1982; Huey and Hertz, 1984; Huey and Bennett, 1987; Van Berkum, 1988), endurance running (eg. Garland *et al.*, 1990), jumping (eg. Losos and Irschick, 1996), climbing (eg. Sinervo and Losos, 1991; Losos and Irschick, 1996), sand-diving (Arnold, 1994, 1995), swimming (Gans, 1977; Heatwole, 1990) and gliding (Marcellini and Keefer, 1976; Losos *et al.*, 1989). However, the majority of these have received little attention and most study has focused on sprint speed and endurance capacity.

This chapter presents an investigation of a number of the performance abilities of the study species of *Niveoscincus* and *Pseudemoia entrecasteauxii*, focusing on sprint speed, jumping and climbing. A number of locomotory behaviours performed by *Niveoscincus* individuals were recorded in the field (Chapter 5). Species that inhabited the dolerite boulder fields, such as *N. greeni*, were observed to run and jump, while the arboreal species, such as *N. pretiosus*, predominantly climb. Thus, sprinting, jumping and climbing provide three ecologically relevant measures of performance ability in *Niveoscincus*.

The only previous research to have examined the performance abilities of *Niveoscincus* was my earlier research on *N. metallicus* and *N. microlepidotus* (Melville, 1994). The

present study provides the first opportunity to conduct a comparative investigation of ecologically relevant performance abilities in Tasmanian skinks.

6.2 Materials and Methods

Performance abilities, such as sprint speed, are affected by a number of factors, such as the reproductive stage of females (Shine, 1980; Bauwens and Thoen, 1981; Garland and Arnold, 1983; Huey *et al.*, 1984; Seigel *et al.*, 1987), recent ingestion of food (Garland and Arnold, 1983; Huey *et al.*, 1984), body temperature (Huey and Slatkin, 1976; Huey *et al.*, 1989), and tail length (Vitt, 1983; Arnold, 1990). Consequently, all the lizards used for the measurement of performance abilities were adults with intact tails and all females were non-gravid. Lizards were not fed prior to any measurement of performance ability.

6.2.1 Sprinting ability

The optimal temperature for the performance experiments was established by sprinting lizards at a range of temperatures. Running data were obtained over a lizard's entire range of activity temperatures, allowing performance curves to be constructed. Sprint speed was measured at fixed temperatures (17, 20, 22, 24, 26, 28, 30, 32°C); the lizards were run at these temperatures in randomised order. A heated race track and a lizard heating device were designed and developed especially for this experiment. The track was 2.5 m long with a metal bottom, lined with sandpaper to allow traction. The track sat on a large box which contained 3 x 120 watt spot lights. A temperature probe attached to the under-side of the track was linked to a controller box which switched the spot-lights on when the temperature dropped below the preset required temperature. The same thermostat arrangement switched the lights off once the required temperature had been reached. This allowed the track to be heated rapidly and maintained to within 1°C of the required temperature. Three light beams at 50 cm intervals, attached to a Macintosh computer, allowed sprint times over 50 cm to be

recorded. Thus, each sprint run had the capacity to generate a maximum of 2 estimates of sprint speed.

The lizards were warmed in a metal container immersed in a water bath. The water temperature was controlled by a heater and thermostat to ± 1°C and the water was continually mixed by a small propeller. The metal container was partitioned so that four lizards could be heated a once, while remaining completely isolated. This method of raising lizard body temperature has advantages over many other methods, which involve heating from one surface, as temperature is less variable.

Animals were warmed in the water bath for at least 30 mins before each sprint trial. They were subsequently chased down the track by repeated taps on the tail with a clear plastic rod which did not trigger the light beams. This protocol has been used many times and was described by Huey (1982). Each lizard was raced three times at each temperature and only one of the set temperatures was trialed each day. The fastest recorded time was considered the maximal speed at that temperature.

After all the trials were completed one side of the race track was removed to allow the lizards to be video taped from a lateral position while sprinting. Two individuals of each species were taped while running down the track. This allowed a simple comparison of the running behaviour of the species.

The optimal temperature for sprinting for each species was also used to measure jumping and climbing. The lizards were heated to their optimal performance temperature (Table 6.1) for 30 mins before all performance trials.

6.2.2 Jumping Ability

Jump distance was measured by inducing each lizard to leap off a horizontal platform 25 cm above the substrate. The platform was over-hung on all sides to prevent the lizards from climbing down. The platform was placed in the centre of a 2 x 1.5 m box

with a 5 cm layer of sand as substrate. An impression was left in the sand as each lizard landed after jumping, allowing easy measurement of jump length. Jumps were measured along the ground from the outer edge of the platform to the sand impression left by the lizard (i.e. as horizontal distance).

Lizards were only jumped once each day and at least one day separated successive jumps. All jumps were conducted at the optimum sprint temperature for the species. Each lizard was jumped three times in total and the longest jump was used as the maximum jump distance for an individual. Lizards were induced to jump by being tapped on the tail and any refusal to jump was recorded. A subject that refused to jump after four taps was returned to the heating container, as body temperature dropped significantly after 30 seconds on the platform.

Four individuals of both *N. greeni* and *N. ocellatus* were induced to jump a distance between two platforms at the same horizontal level. The two platforms were separated by 15 cm. This allowed the jumps to be video taped to examine the body posture of the lizard during the leap. No other species could be induced to jump reliably under these circumstances.

6.2.3 Climbing Ability

Wooden rods were roughened with coarse sandpaper to provide traction. Climb speed was measured on a rod with a diameter of 2.5 cm. Trials were conducted in a 2 x 1.5 m box with a 5 cm layer of sand as substrate. The rod was angled at 45° and speed was measured over a 50 cm distance with a stopwatch. Climbing trials were conducted at the optimum sprint temperature for the species. Speed was then calculated as centimetres per second. Trials were excluded from the data if the lizards refused to run, jumped from the rod or fell off. However, the occurence of these events was recorded. Lizards were run once per day, with at least one day between trials.

Table 6.1 Performance abilities, optimal temperature for performance and snout-vent lengths for seven *Niveoscincus* species and *Pseudemoia entrecasteauxii* (values are means ± standard error)

	n	Snout-vent Length (mm)	Optimal Temperature (°C)	Sprint Speed (m/sec)	Jump Distance (cm)	Climb Speed (cm/sec)
N. coventryi (Mt St Leonards)	20	46.8 ± 0.78	28.0 ± 0.26	0.39 ± 0.021	12.2 ± 0.35	2.6 ± 0.04
N. greeni (Ben Lomond)	29	58.2 ± 1.28	27.8 ± 0.29	0.89 ± 0.055	31.9 ± 0.72	3.0 ± 0.21
N greeni (Mt Pelion East)	23	60.8 ± 0.85	28.3 ± 0.49	0.90 ± 0.060	34.1 ± 0.80	3.1 ± 0.20
N. metallicus (Clarence Lagoon)	30	53.4 ± 0.55	26.1 ± 0.36	0.50 ± 0.047	15.9 ± 0.54	3.2 ± 0.06
N. metallicus (Orford)	19	50.9 ± 1.03	26.9 ± 0.48	0.54 ± 0.045	15.8 ± 0.73	3.0 ± 0.07
N. microlepidotus (Mt Hartz)	20	55.1 ± 1.37	26.6 ± 0.53	0.51 ± 0.078	25.8 ± 0.94	3.0 ± 0.10
N. microlepidotus (Mt Wellington)	21	55.8 ± 0.90	25.6 ± 0.29	0.46 ± 0.043	24.4 ± 0.82	3.2 ± 0.07
N. ocellatus (Lake Augusta)	20	70.9 ± 1.08	28.0 ± 0.29	0.92 ± 0.057	38.0 ± 0.72	2.1 ± 0.13
N. ocellatus (Orford)	27	58.9 ± 0.85	27.0 ± 0.23	0.72 ± 0.052	33.6 ± 0.90	2.6 ± 0.09
N. orocryptus (Mt Eliza)	20	49.0 ± 2.17	27.1 ± 0.77	0.55 ± 0.068	18.9 ± 1.23	4.1 ± 0.33
N. orocryptus (Mt Hartz)	29	55.2 ± 1.27	27.0 ± 0.46	0.67 ± 0.032	25.5 ± 0.94	3.0 ± 0.07
N. pretiosus (Clarence Lagoon)	18	47.2 ± 0.46	28.2 ± 0.45	0.45 ± 0.027	18.9 ± 0.76	4.6 ± 0.48
N. pretiosus (Pirates Bay)	22	48.0 ± 0.91	27.9 ± 0.57	0.48 ± 0.032	16.1 ± 0.54	4.2 ± 0.36
P. entrecasteauxii (Hobart)	15	46.8 ± 0.37	29.6 ± 0.51	0.26 ± 0.028	10.1 ± 0.62	2.5 ± 0.05

6.3 Results

6.3.1 Optimal Temperature for Performance

Optimal temperatures for locomotory performance are listed in Table 6.1. Locomotory performance trials were conducted at 26, 28 or 30°C depending on the optimal temperature for sprinting in each species. *Niveoscincus metallicus* and *N. microlepidotus* were run at 26°C. *Niveoscincus greeni, N. coventryi, N. ocellatus, N. orocryptus* (Mt Hartz), *N. orocryptus* (Mt Eliza) and *N. pretiosus* were trialed at 28°C. *Pseudemoia entrecasteauxii* was the only species in which locomotory performance was tested at 30°C.

6.3.2 Ecomorphs in Performance Trials

It was found that, as in Chapter 4, there were three distinct ecomorph types when each performance ability was considered seperately. These groups were identified as saxicolous (*N. greeni, N. ocellatus, N. microlepidotus* and *N. orocryptus* (Mt Hartz)), ground-dwelling (*N. metallicus, N. coventryi* and *P. entrecasteauxii*) and arboreal (*N. pretiosus* and *N. orocryptus* (Mt Eliza)).

The saxicolous ecomorph could be divided into two groups if overall performance ability was considered (Table 6.1): saxicolous (*N. greeni* and *N. ocellatus*) and heath/rock-dwelling species (*N. microlepidotus* and *N. orocryptus* (Mt Hartz)). The saxicolous species were found have high performance abilities in sprinting and jumping, yet only moderate ability in climbing. The heath/rock-dwelling species had moderate abilities in all performances recorded. As this chapter considers each performance trait seperately the analyses were conducted using three ecomorph groups. A discussion of overall performance ability can be found in Chapter 8.

6.3.3 Sprinting

The mean maximum sprinting speed varied significantly between species ($F_{6,255}$ = 28.87; $p < 0.001$). The species with the fastest mean maximum sprint speed were *N. ocellatus* and *N. greeni*, while the slowest was *Pseudemoia entrecasteauxii* (Table 6.1). The slowest species of *Niveoscincus* was *N. coventryi*, which was approximately 3 times slower than the maximum mean sprinting speed recorded for *N. ocellatus* (Central Plateau). The species were grouped according to ecomorph type: ground-dwelling (*N. metallicus, N. coventryi, P. entrecasteauxii*); arboreal (*N. pretiosus, N. orocryptus* (Mt Eliza)); and saxicolous (*N. greeni, N. ocellatus, N. microlepidotus, N. orocryptus* (Mt Hartz)). The maximum sprinting speeds of the ecomorph types varied significantly (F-ratio$_{2,259}$ = 37.71; $p < 0.001$), as did those of the populations of *N. ocellatus* ($F_{1,44}$ = 7.85; $p = 0.008$).

Mean maximum sprint speed was significantly and positively related to snout-vent length ($p < 0.001$) (Figure 6.1). Consequently, regression analysis was applied to the data before sprinting speed was included in the comparative analysis in Chapter 8.

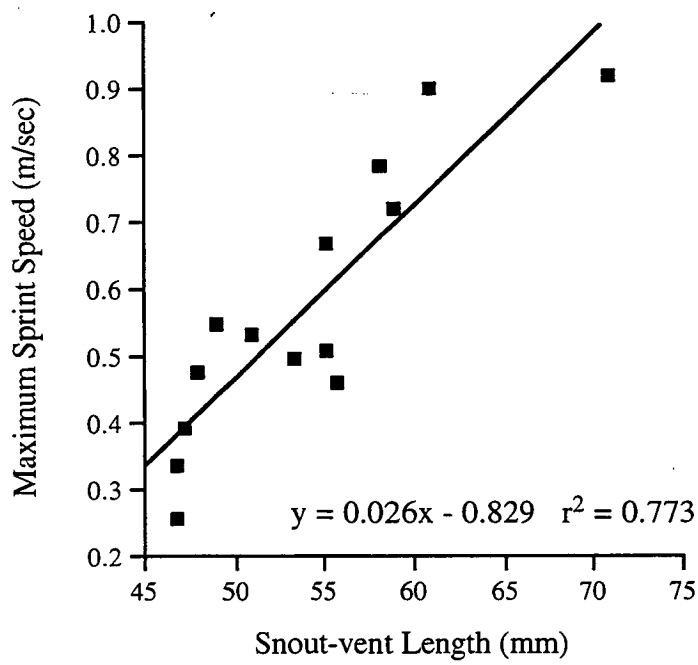


Figure 6.1 Least squares linear regression of mean sprint speed vs snout-vent length in all study species (data taken from Table 6.1).

Video Analysis

Differences in the running styles employed by the species studied were apparent. The ground-dwelling species such as *N. metallicus* held their bodies close to the running surface and used sinusoidal movements of the body and tail when sprinting maximally. The saxicolous/heath dwelling and arboreal species, such as *N. microlepidotus* and *N. pretiosus*, tended to run with their head and front of the trunk held above the ground and sinusoidal movements were not employed as much as they were by the ground-dwelling species. The two species that sprinted the fastest, the saxicolous species *N. greeni* and *N. ocellatus*, were observed to "leap" down the track when running maximally (Plate 6.1). These species also ran with their body held at an average angle of 10° ± 3.5 when sprinting at close to their maximum speed (>0.70 $m.s^{-1}$). The tail and whole trunk was held above the track surface and often only one leg touched the substrate at any moment. A very brief "rest" period followed each "leap", during which the lizards would stop and their entire body was in contact with the track surface (Plate 6.1).

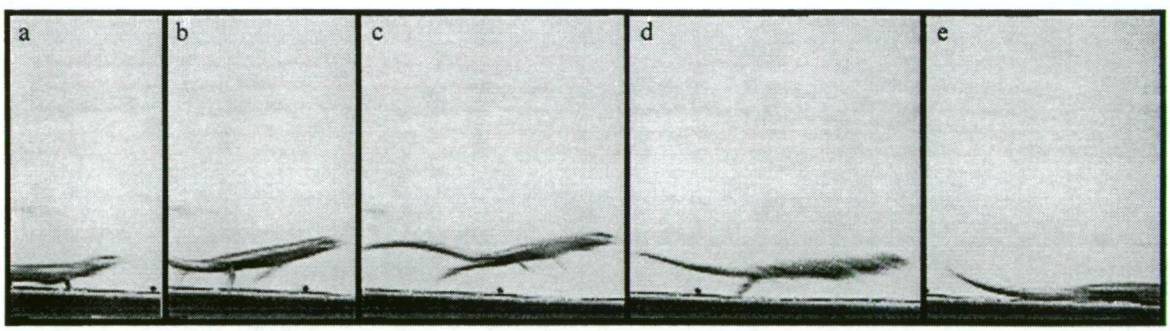


Plate 6.1 Sequence of video-stills showing an individual of *N. greeni* sprinting down the track. The lizard leaps down the track, leaving the ground in frame (c) and returning to the track in (d). After returning to the ground the lizard rests briefly (frame (e)), before moving on. The rear legs propel the lizard down the track (frame (b)), with the front legs rarely touching the ground.

6.3.4 Jumping

The mean maximum jump distance varied significantly between species ($F_{6,291}$ = 172.58; $p < 0.001$). The longest mean jump distances were achieved by *N. ocellatus*

and *N. greeni*, while the poorest jumper was *Pseudemoia entrecasteauxii* (Table 6.1). The shortest mean jump distance recorded in *Niveoscincus* was for *N. coventryi*, and the distance jumped by this species was approximately 3 times less than the longest mean jump distance recorded for *N. ocellatus* (Central Plateau). When the species were grouped according to ecomorph type (ground-dwelling: *N. metallicus, N. coventryi, P. entrecasteauxii*; arboreal: *N. pretiosus, N. orocryptus* (Mt Eliza); and saxicolous: *N. greeni, N. ocellatus, N. microlepidotus, N. orocryptus* (Mt Hartz)), there was a significant difference between the maximum jump distance of ecomorph types ($F_{2,295}$ = 272.24; $p < 0.001$). There was a significant difference between the populations of *N. ocellatus* ($F_{1,45} = 12.84$; $p = 0.001$) and *N. pretiosus* ($F_{1,38} = 8.99$; $p = 0.005$).

Mean maximum jump distance was significantly related to snout-vent length ($p < 0.001$), with jump distance increasing with snout-vent length (Figure 6.2). Consequently, a regression analysis was applied to the data before jump distance was included in the comparative analysis in Chapter 8.

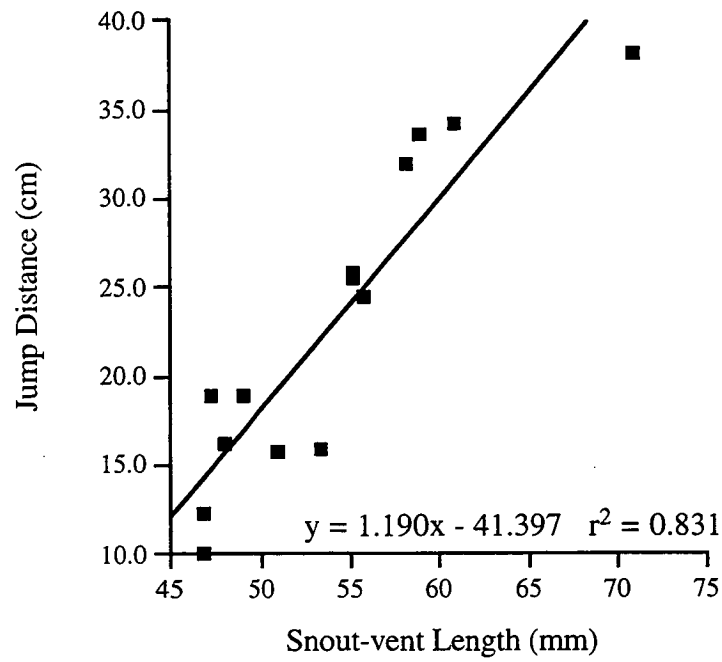


Figure 6.2 Least squares linear regression of mean jump distance vs snout-vent length in all study species (data from Table 6.1).

Motivation

The number of times a lizard jumped off the platform after only a single tap on the tail was recorded (Table 6.2) as an index of the willingness to jump. There were very large differences between the species. The two saxicolous species, *N. ocellatus* and *N. greeni*, often did not require any encouragement to jump, and as soon as they were placed on the platform they would immediately leap off it. The majority of the species would jump off the platform with minimal encouragement (1 tap) in 40 - 75% of trials. In these species there was often large variation between individuals (Table 6.2). The two arboreal species, *N. pretiosus* and *N. orocryptus* (Mt Eliza), rarely jumped readily; often they refused to jump within the 30 second time limitation and had to be returned to the heating container. These species showed quite different behaviour to the other species; when placed on the platform they would often flatten their body to the surface and grip the edge of the platform with their feet.

Table 6.2 The percentage of times individual lizards from each species would jump after a single tap on the tail

Species	Site	n	% lizards jumping immediately (± s.e.)
N. coventryi	Mt St Leonards	20	45 ± 10.6
N. greeni	Ben Lomond	29	95 ± 1.7
N. greeni	Mt Pelion East	23	98 ± 2.1
N. metallicus	Clarence Lagoon	30	60 ± 12.1
N. metallicus	Orford	19	65 ± 8.9
N. microlepidotus	Hartz Mtn.	20	63 ± 9.1
N. microlepidotus	Mt Wellington	21	65 ± 13.1
N. ocellatus	Lake Augusta	20	97 ± 1.6
N. ocellatus	Orford	27	98 ± 4.9
N. orocryptus	Mt Eliza	20	20 ± 6.7
N. orocryptus	Hartz Mtn.	29	65 ± 11.5
N. pretiosus	Clarence Lagoon	18	15 ± 5.1
N. pretiosus	Pirates Bay	22	12 ± 7.5
P. entrecasteauxii	Hobart	15	42 ± 12.3

Video Analysis

Video footage of 15 cm jumps by four individuals of both *N. greeni* and *N. ocellatus* were analysed. Jumps could be divided into four segments: (1) hindlimb cycle (bring one hindlimb forward); (2) contract body, bending spine; (3) leap; and (4) landing. During the hindlimb posturing one of the hindlimbs is brought forward (Plate 6.2), bringing the hind foot close to the ipsilateral forelimb. Bending of the trunk decreases the spine length by 26 ± 2.1% from the initial body posture (Plate 6.2). As the lizard begins the takeoff phase, the forelimbs leave the platform surface first and the head is held above the level of the shoulders. The angle of the body in relation to the platform changes rapidly as the forelimbs leave the platform. The hindlimbs are extended rapidly and the lizard leaves the platform surface. The hindlimbs are subsequently held in line with the trunk. In the flight of the jump the trunk is hyper-extended (Plate 6.2), and the spine length increases from the initial body posture by 19 ± 1.5%. In this flight phase the limbs and head are held in line with the trunk, making the body more spindle shaped (Plate 6.2). The angle of the body during flight is 28° ± 3.6. Towards the end of flight the limbs are extended (Plate 6.2) for landing. The angle of the body remains around 30° throughout the jump, and the body does not angle down towards landing.

A number of different types of landing were observed. If the lizard was landing on the flat surface of the platform the hindlegs would land first, followed by the forelimbs. More commonly the animals landed on the edge of the platform (Plate 6.3). On these occasions the forelimbs would grip the corner of the platform and the rest of the trunk would swing down and the body would come into contact with the side of the platform. The lizard would then climb onto the top of the platform and move off. During this type of landing the angle of the trunk tended to increase to 35° ± 3.5 just prior to contact.

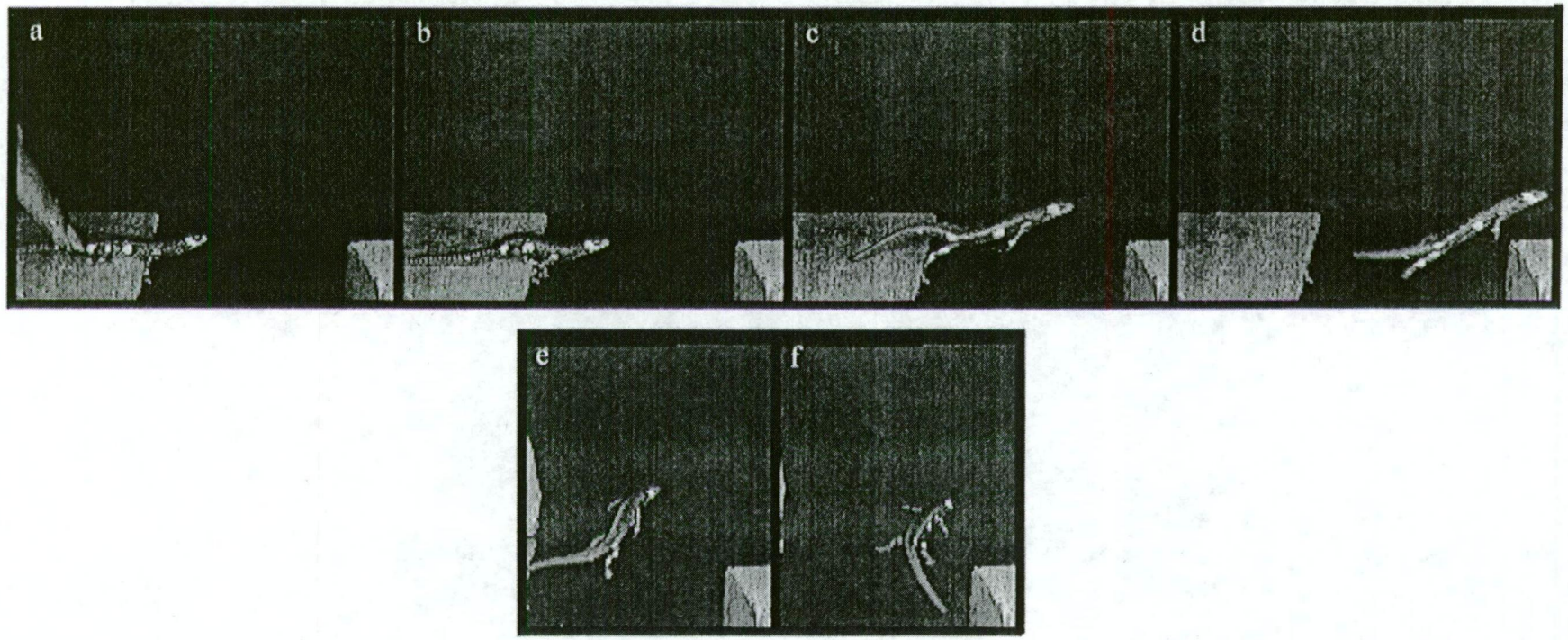


Plate 6.2 Sequence of video-stills showing jump of an individual of *N. greeni*. Frames (a) to (d) show a lateral view of a jump, while frames (e) and (f) show a dorsal view. In frames (a) and (b) lizard moves one hindleg forward (the one closest to the camera) and the spine bends in preparation for the jump. The lizard propels itself off the platform by rapidly extending its hindlegs, frame (c). During flight the lizard holds its limbs beside the body, frames (d) and (e), giving it a "spindle" shape. Prior to landing the legs are extended, frame (f).

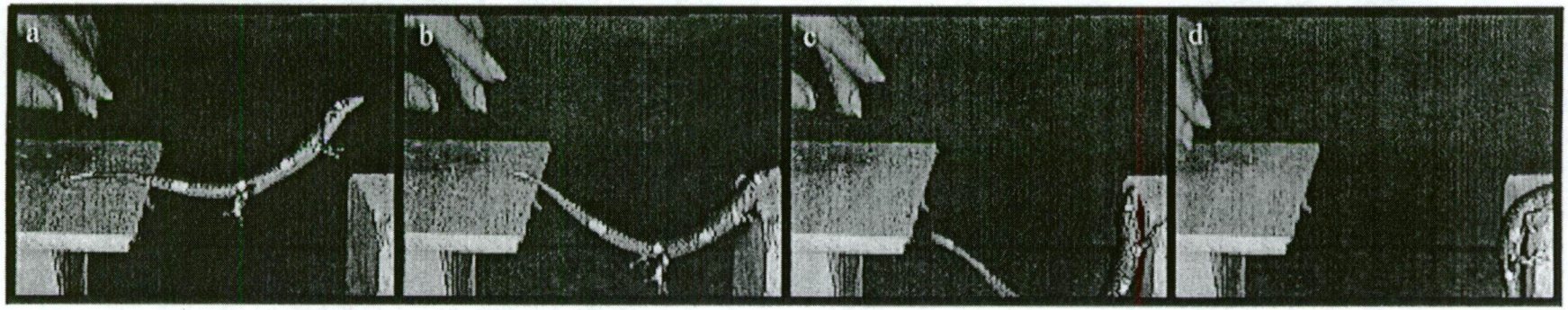


Plate 6.3 Sequence of video-stills showing a landing sequencing in a jump of an individual of *N. ocellatus*. The forelimbs were stretched out, frame (a), in preparation for landing. The forelimbs first make contact with the edge of the landing brick, frame (b), and the rest of the body comes in contact with the side of the brick, frame (c). The lizard then climbs to the top of the brick, frame (d).

The jumps analysed were the ones where the lizard landed on the platform without problems. A number of the jumps were very inaccurate, and 19 ± 3.5% missed the landing platform. Sometimes the lizards overshot the platform, only their hindlegs coming into contact with the surface, and they fell off the other side of the platform. In other cases the jump fell short, the lizards were unable to grip the corner of the platform sufficiently, and they fell to the ground. It was also observed that when the lizards extended their legs for landing their body became unstable and often wobbled in flight.

6.3.5 Climbing

Mean maximum climb speed varied significantly between species ($F_{6,291} = 106.73$; $p < 0.001$). The species with fastest mean climb speed was *N. orocryptus* (Mt Eliza) and *N. pretiosus*, while the slowest was *Pseudemoia entrecasteauxii* (Table 6.1). The slowest mean climb speed recorded in *Niveoscincus* was for *N. coventryi*, and the climbing speed of this species was approximately 3 times slower than the fastest mean climb speed recorded for *N. pretiosus* (Clarence Lagoon). When the species were grouped according to ecomorph type as before there was a significant difference in the maximum climb speed ($F_{2,295} = 513.55$; $p < 0.001$). There were no significant differences in climb speed between the populations of any of the species tested.

Although there was no significant relationship when mean maximum climb speed of each species was regressed against mean snout-vent length, a significant relationship did exist when all individual values were analysed (Figure 6.8, $p < 0.001$). Climb speed tends to decrease with snout-vent length (Figure 6.3). Consequently, a regression analysis was applied to the data before climb speed was included in the comparative analysis in Chapter 8.

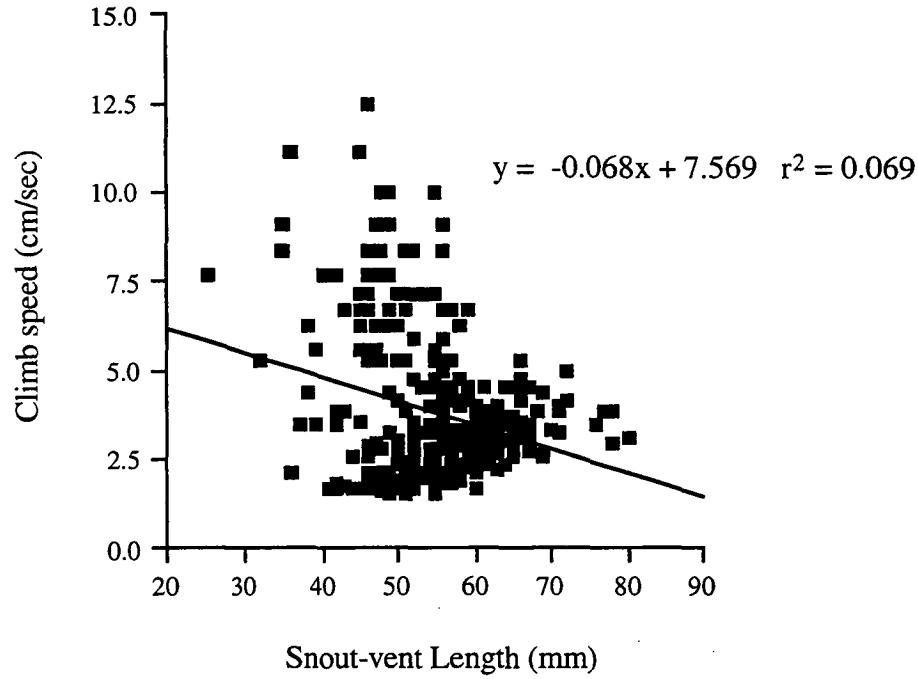


Figure 6.3 Least squares linear regression of maximum climb speed vs snout-vent length in all individuals studied.

Motivation

Each time a lizard jumped or fell off the climbing rod this was recorded (Table 6.3). There were significant differences between the species in both jumping ($F_{6,291}$ = 155.25; $p < 0.001$) and falling ($F_{6,291}$ = 123.17; $p < 0.001$). The two saxicolous species, *N. ocellatus* and *N. greeni*, jumped off the climbing rod in approximately 50% of the trials. As soon as they were placed on the rod they would immediately leap off it. When these species did climb they appeared to have difficulty gripping the rod. In order to do so, they had to bring their legs under their body, and this appeared to be particularly difficult for larger lizards.

Most species, however, would not jump off the rod in all trials. The only other species observed to leap off the climbing rod was *N. orocryptus* (Mt Hartz) but this was relatively uncommon.

The ground-dwelling species, *N. metallicus, N. coventryi* and *P. entrecasteauxii,* fell off the rod frequently. They appeared to have difficulty grasping the wooden rod and

when they started to climb the sinusoidal movement of their trunk would unbalance them.

The two arboreal species, *N. pretiosus* and *N. orocryptus* (Mt Eliza), would start climbing immediately after being placed on the rod, only two diagonally opposite limbs leaving the rod at the same time. They kept their bodies close to the rod and often curled their tails around the rod while climbing.

Table 6.3 The mean number of times individual lizards from each species jumped or fell off the climbing rod in all trials

Species	Site	n	falls (± s.e.)	jumps (± s.e.)
N. coventryi	Mt St Leonards	20	4.5 ± 0.46	0.0
N. greeni	Ben Lomond	29	0.0	4.9 ± 0.33
N. greeni	Mt Pelion East	23	0.5 ± 0.04	4.6 ± 0.31
N. metallicus	Clarence Lagoon	30	2.9 ± 0.30	0.0
N. metallicus	Orford	19	2.5 ± 0.35	0.0
N. microlepidotus	Hartz Mtn.	20	0.4 ± 0.15	0.0
N. microlepidotus	Mt Wellington	21	0.2 ± 0.12	0.0
N. ocellatus	Lake Augusta	20	0.0	4.3 ± 0.26
N. ocellatus	Orford	27	0.2 ± 0.12	4.8 ± 0.22
N. orocryptus	Mt Eliza	20	0.0	0.0
N. orocryptus	Hartz Mtn.	29	0.1 ± 0.06	1.2 ± 0.18
N. pretiosus	Clarence Lagoon	18	0.0	0.0
N. pretiosus	Pirates Bay	22	0.0	0.0
P. entrecasteauxii	Hobart	15	5.3 ± 0.38	0.0

6.4 Discussion

6.4.1 Sprinting ability

Maximum sprint speed is generally accepted as an ecologically relevant performance measurement (eg. Huey and Bennett, 1987; Hertz *et al.*, 1988; Garland and Losos, 1994). It has been reported that variation in sprinting ability may affect survival probabilities within populations of reptiles (Christian and Tracy, 1981).

The current study has shown that running is a frequent mode of locomotion in all species of *Niveoscincus* (Chapter 5). There is significant variation between the species in their sprinting ability. The saxicolous species, *Niveoscincus greeni* and *N. ocellatus*, are able to run significantly faster than the ground-dwelling, arboreal and heath/rock dwelling species. However, running style and body size appeared to have a strong effect on the running ability of each species.

Sprint speed is the most commonly studied aspect of reptilian locomotor abilities, and a considerable body of research addresses the mechanistic basis of variation in sprinting. The pattern of movements of the hindlimb has been greatly modified during the evolution of reptiles (Brinkman, 1981). In the primitive pattern the femur usually projects laterally from the body and is moved in a horizontal arc, associated with sigmoidal bending of the vertebral column. The ground-dwelling species, *N. coventryi*, *N. metallicus,* and *P. entrecasteauxii*, were all observed to move their body sinusoidally while sprinting. Lateral undulation of the body has been found to be an important component in the production of locomotor thrust in other lizards, such as the gekkonine geckos (Russell and Bauer, 1988).

In contrast, the saxicolous species of *Niveoscincus* do not use significant lateral movement of their bodies while running. Instead, they leap while sprinting at their maximum capacity. In a similar fashion *Anolis* lizards often hop when they are sprinted on a horizontal race track, and consequently they were run on a horizontal race track inclined at 37° to prevent this behaviour (Losos, 1990). This style of locomotion may give an advantage in escape behaviour in a rocky environment, when leaping over an uneven substrate would presumably increase the speed of escape. Running with as little of the body touching the substrate as possible is also an efficient means of increasing speed by reducing drag.

Biomechanical models predict a positive relationship between body size, relative limb length and sprint speed (Marsh, 1988; Losos, 1990b). Most cursorial mammals have elongated legs, primarily as a result of the increased length of the distal elements (Biewener, 1990). Cursorial lizards also exhibit elongated limbs, but all limb elements appear to increase with no apparent patterns (Rieser, 1977). The morphological differences between *Niveoscincus* species will be discussed in Chapter 7.

6.4.2 Jumping ability

Jumping and leaping in animals is well known and has been extensively studied in, for example, frogs (eg. Calow and Alexander, 1973; Zug, 1978; Emerson, 1985; Lutz and Rome, 1994), dogs (Alexander, 1974) and prosimians (Oxnard *et al.*, 1981). A number of different types of jumping have been described in vertebrates: the vertical jump of frogs (Calow and Alexander, 1973); the high and long jump in dogs (Alexander, 1974); and the bipedal leaps of some mammal species (Hall-Craggs, 1965; Alexander and Vernon, 1975). It is less commonly known that some reptiles, for example crocodiles and many lizards, employ jumping to move, display or capture prey (Moermond, 1981; Bels and Theys, 1989). Moermond (1979) and Pounds (1988) described jumping as a frequent mode of locomotion in anolid lizards.

My study has shown that jumping is a frequent mode of locomotion in some species of *Niveoscincus* (Chapter 5), especially the saxicolous species *Niveoscincus greeni* and *N. ocellatus.* There was significant variation between the species in their jumping ability. The saxicolous and heath/rock dwelling species could jump significantly further than the other species, while the ground-dwelling and arboreal species appeared to be able to jump short distances only. However, motivation and body size seem to have a strong effect on the jumping ability of the species.

Jumping in small animals is limited by their ability to produce power, but this problem can be overcome by increasing the relative length of the jumping legs (Gabriel, 1984). Thus, it is possible that *Niveoscincus greeni* and *N. ocellatus* are able to jump further

than the other species because the have relatively longer legs than the other species. The morphological differences between the species will be examined in Chapter 7.

The biomechanics of jumping have been examined only rarely in lizards, for example in a legless lizard (Bauer, 1986) and in *A. carolinensis* (Bels *et al.*, 1992). Jumping in *Anolis carolinensis*, unlike frogs and mammals, has a phase of hindlimb posturing and a relatively constant but low angle of the body during the jump. The takeoff angle of *A. carolinensis* was always close to 30° for a jumping distance of 10 to 30 cm. In the strongest jumps recorded in the frog *Rana temporaria* its feet left the platform at about 55° to the horizontal (Calow and Alexander, 1973).

The kinetic energy for a jump with a takeoff angle of 30° does not differ from that at an angle of 45°. However, the distance which can be jumped with a takeoff angle of 45° is much farther (Gabriel, 1984). Bels *et al.* (1992) suggest that, as the jumps recorded in *A. carolinensis* were escape jumps, a lower angle of takeoff may be an advantage because it reduces the duration of the jump. Thus, the period of time exposed to potential predators is reduced without a significant increase in energy expended. It has also been suggested that a low angle of takeoff would reduce the chance of coming into contact with low bushes (Bels *et al.*, 1992). However, this would not be a factor for the saxicolous species of *Niveoscincus*, as they occupy microhabitats with little or no low vegetation.

During takeoff storage and recovery of energy is likely to involve two mechanisms. Firstly, energy is stored when the vertebral column is shortened. This energy is subsequently recovered during initial takeoff, when the body is extended. Secondly, energy storage will occur in the hindlimb elastic structures and recovery during the takeoff phase (Bels *et al.*, 1992).

Takeoff in *Niveoscincus greeni* and *N. ocellatus* differs from that described for *Anolis carolinensis* as they move only one hind leg forward into the takeoff position. *Anolis*

species use rapid simultaneous extension of the hindlimbs for propulsion during jumping (Pounds, 1988). *Anolis carolinensis* has a phase of hindlimb posturing where the rear legs perform a circumduction movement, so that the hindfeet are placed ahead of the forefeet (Bels and Theys, 1989). It it possible that bringing only one leg forward in *N. greeni* and *N. ocellatus* allows a more rapid takeoff than if both hind legs were brought forward.

The elevated head during takeoff may influence the elevation of the body, takeoff angle and pitch (Bels *et al.*, 1992). Most jumping species show a shortening of the trunk which prevents pitching in a forward direction. *Niveoscincus greeni* and *N. ocellatus* are more elongated than jumping animals, such as frogs, and may overcome forward pitching during takeoff by prior elevation of the head and shoulders. The centre of mass may also be placed posteriorly to prevent pitch, as is the case in *Anolis carolinensis* (Bels *et al.*, 1992).

Both *Niveoscincus greeni* and *N. ocellatus* are saxicolous and the dolerite surfaces they land on are usually very uneven. The low angle of jump that they maintain throughout the jump may provide an advantage when landing on angled surfaces. These lizards appear to be able to alter their landing behaviour, using either the rearlegs or their forelimbs, depending on the surface.

The tail did not appear to be important in jumping in any of the *Niveoscincus* species or in *P. entrecasteauxii*, as it passively followed the body in all cases. However, specimens of *Anolis carolinensis* reportedly have difficulty in jumping when their tails are experimentally removed (Ballinger, 1973).

6.4.3 Climbing ability

Sprint speed, clinging ability and agility are all affected by support diameter (Losos and Sinervo, 1989; Sinervo and Losos, 1991; Losos *et al.*, 1993; Losos and Irschick, 1996). For example, sprint speed was found to decline on smaller perch sizes for

anolids (Losos and Sinervo, 1989). Terrestrial populations of *Scleroporus occidentalis* run faster on broader surfaces and are more severely affected by decreasing diameter, running more slowly on narrow surfaces, than are arboreal populations (Sinervo and Losos, 1991).

Climbing on narrow surfaces is a frequent mode of locomotion in the arboreal species *Niveoscincus pretiosus* and *N. orocryptus* from Mt. Eliza (Chapter 5). This chapter has indicated that there are significant differences in the climbing abilities of the species of *Niveoscincus*. The arboreal species are able to climb significantly faster than the other species, while the ground-dwelling species have very limited climbing abilities, often falling from the wooden rod used for testing. The saxicolous species possess the ability to climb but showed a preference for jumping from the test rod. Motivation and body size seemed to have a strong influence on the climbing behaviour of the species.

Firm footing and surefootedness facilitate climbing. Many adaptations have been found in climbing animals; for example, many frogs use capillarity, and some possess peg-like projections on the outer epidermal cells of the toe discs, to stick to surfaces (Emerson and Diehl, 1980). *Pransinohaema virens*, an arboreal skink, differs from its closest relatives in that it exhibits subdigital adhesive setae. These setae are similar to those found in some species of *Anolis* in shape and are similar in size to the subdigital lamellae of many geckos. The other species of *Pransinohaema* have pad scales which are folded and ruffled. Consequently, there are two lineages of epidermal specialisation within this small radiation (Williams and Peterson, 1982). It is possible, therefore, that the arboreal species, *Niveoscincus pretiosus* and *N. orocryptus* (Mt. Eliza), have also evolved some morphological features, such as an increase in the size of sub-digital lamellae, to enhance their surefootedness. However, I did not investigate this possibility.

6.4.4 Motivation and maximal performance

The distinction between performance and behaviour is not always clear. How can it be determined if a lizard is running at its morphological, physiological or biochemical limits? Motivational differences between individuals are clearly possible, and may be very important, in performance measurements. A number of factors are known to affect sprinting performance, including morphology, physiology and behaviour (Garland, 1985; Losos, 1990; Garland and Losos, 1994). The usual solution to overcome motivational problems is to employ repeated testing of individuals and use the fastest trial as a measurement of maximal speed (eg. Hertz *et al.*, 1983; van Berkum, 1988; Van Damme *et al.*, 1989; Sinervo *et al.*, 1991). Despite the fact that this was the approach taken in this study, there were still behavioural differences apparent between the species.

Organisms typically possess a range of traits that confer performance advantages in the environment in which they usually exist (Arnold, 1983). Thus, it is probable that a lizard will possess a number of behavioural responses to a given situation. For example, the arboreal species *Niveoscincus pretiosus* will move rapidly to escape on a flat track or wooden rod but will often refuse to move when place on a raised platform. Presumably this unwillingness to jump from heights serves to protect individuals from injuring themselves by falling from heights. The data obtained for *Niveoscincus* suggest that the escape behaviour of a species depends upon the microhabitat it occupies. The arboreal species *N. pretiosus* often refuses to jump, while the saxicolous species *N. greeni* will rarely climb, preferring to jump.

Losos and Irschick (1996) considered the effect of substrate on two methods of escape, running and jumping, and found that 5 species of anolid lizards altered their escape behaviour to use the more effective means of escape. However, it appears that in *Niveoscincus,* the capacity to alter escape behaviour is species dependent. Those species found in a range of microhabitats, such as *N. microlepidotus* and *N. orocryptus* (Mt Hartz), resembled anolids in the ability to change their escape behaviour to suit the substrate. Those species with a more restricted range of microhabitat, such as *N.*

greeni, had obvious difficulty in using climbing as an escape behaviour. This may be a result of morphological restrictions, and *N. greeni* may find it difficult to grip the relatively narrow wooden rods used for testing because it has relatively long legs. The morphological differences between the species will be discussed in Chapter 8.

6.4.5 Allometry and performance

The invasion and exploitation of the earth's terrestrial environments has yielded a diverse range of animals that share a common problem of movement. This diversity is manifest in size, morphology, locomotor performance and skeletal materials (Biewener, 1990). Size and shape are fundamental characters of any organism and would be expected to influence whole body performance characteristics (Garland, 1985).

An incremental increase in locomotor ability with increasing body size has been reported in many ectothermic vertebrates (Bennett *et al.*, 1989). Body size affects many traits, including performance capacities. Sprint speed is the most commonly studied performance ability in lizards, and a considerable amount of work has examined the mechanistic basis of variation in sprinting. Differences in body size and relative limb length seem to be the most important causal factors (Garland and Losos, 1994). There was a significant positive relationship between body size and sprint speed in *Niveoscincus.* The larger species, such as *N. ocellatus,* were able to sprint much faster than the smaller species, such as *N. coventryi*. A similar relationship has been reported in many other lizards species. For example, the variation in performance ability in the species of *Anolis* results from differences in body size (Losos, 1990). Similarly, Gleeson and Harrison (1988) found that approximately 50% of the variation in sprint speed in the desert iguana, *Dipsosaurus dorsalis*, could be attributed to muscle fibre areas and snout-vent length.

Pounds (1988) demonstrated a similar positive correlation between body size and locomotor behaviour, such as jumping. Biomechanical models suggest that body and

muscle mass, limb length, location of the centre of mass, muscle composition and behaviour can affect jumping performance (Emerson, 1985; Pounds, 1988). This relationship has been well studied in a number of frog species (Zug, 1972, 1978; Emerson, 1978) and anolid lizards (Losos *et al.*, 1989). Losos (1990) found that body size and hindlimb length were the most important factors in the evolution of jumping in the genus *Anolis*. A strong positive correlation between snout-vent length and jump distance was also found in *Niveoscincus*.

The speed at which a species can climb was found to be negatively correlated with body size in *Niveoscincus*. The smaller species, such as *N. pretiosus*, are able to climb faster than the larger species, such as *N. greeni*. The relationship between climb speed and snout-vent length was not as strong as the correlation between body size and sprint speed or jump distance, as a number of the smaller species, such as *N. coventryi* and *P. entrecasteauxii*, were very slow climbers. It is possible that other morphological characteristics, such as leg length, affect climbing speed in *Niveoscincus* as strongly as snout-vent length.

Other studies have found that morphological features other than body size affect performance abilities in lizards. For example, the long legged species of *Anolis* jumped relatively farther and ran faster than the shorter legged species, when the effect of body size had been removed (Losos, 1990). Consequently, the effect of body size will be removed before including the data on performance abilities in the comparative analysis presented in Chapter 8.

CHAPTER SEVEN

MORPHOLOGICAL CHARACTERISTICS

7.1 Introduction

The analysis of pattern and process in the transformation of organic design has been a major component of research in systematic and functional biology (Schaeffer and Lauder, 1986). At the beginning of the 19th century the study of morphology was merely the scientific elaboration of laws governing the internal and external structure of organs and organisms, without any concept of the evolutionary transition from one form to another (Duncker, 1985). Charles Darwin provided insight into the hereditary nature of character changes and natural selection in organisms. This allowed the development of a historical and phylogenetic interpretation of the rich variety of form relationships in organisms. However, for much of the 20th century morphology continued as a nonfunctional descriptive science (Duncker, 1985).

One hundred and fifty years after the first productive morphological studies there has been a strong revival (Duncker, 1985). Study has been redirected toward the interpretation of morphology in terms of adaptation and the morphological basis of adaptive radiation (Schaeffer and Lauder, 1986). The modern analysis of morphology has the potential to provide an understanding of the dynamic, functional nature of organisms and their development during phylogeny.

The isolated description of an animal's morphology is of limited use, as morphological structures will reflect ancestral relationships as well as any response to current selection. The former are often referred to as homologies and the latter as analogies (Gans, 1974; Hildebrand, 1995). Comparisons among species allow differentiation between these two, but not exclusive explanations of similarity.

A number of studies of lizard clades have examined the patterns of covariation within a suite of morphological traits to determine the adaptive significance of morphological

diversification (eg., Lauder and Liem, 1989; Losos, 1990a; Miles, 1994). A common feature among coexisting assemblages of lizards is the tendency for divergence in patterns of habitat exploitation among the constituent species (Miles, 1994). Coincident with this pattern is the tendency for the morphology of species to show parallel variation.

The Australian fauna includes a remarkable assemblage of scincid lizards, possessing a wide variety of morphologies (Cogger, 1975). This is due largely to the great variation that occurs in the relative sizes of the limbs, trunk and tail (Greer, 1989). Limbs can vary from well-developed to absent, trunks from short and stout to long and thin, and tails from long to short. Some genera, for example *Anomalopus*, have reduced their hindlimbs much more than the front ones. In contrast, many species of *Lerista* have front limbs that are much more reduced than the hind ones (Gans, 1984). The most common morphological changes observed in Australian skinks are a shortening of the limbs, elongation of the trunk, and either a shortening or lengthening of the tail. These changes are relatively common compared with, for example, changes in head length (Greer, 1989).

The purpose of this chapter is to quantify the morphological characteristics of *Niveoscincus* and *Pseudemoia entrecasteauxii* which are particularly relevant to locomotion, including the length of the bones of the fore- and hindlimbs. This will provide insight into the trends expressed in the evolutionary radiation of morphological characteristics in *Niveoscincus*.

The radiation of morphological characteristics in *Niveoscincus* has not been investigated in detail and existing research is restricted to taxonomic descriptions and qualitative discussions of evolutionary patterns of morphology (Hutchinson and Schwaner, 1989). This study provides the first opportunity to conduct a comparative investigation of morphological features relevant to ecology and locomotory performance and behaviour.

7.2 Materials and Methods

7.2.1 Osteological measurements

At the end of each of the performance experiments (Chapter 6) the snout-vent length of each lizard was measured. Thus, there were three separate measurements of snout-vent length were used to reduce the measurement error. The average of the three measurements was used as the snout-vent length for that individual.

All species of *Niveoscincus* are small to medium sized skinks. Thus, any variation in bone length between species will be very small and measurement must be very precise to pick up any variation in bone lengths. It was decided that measuring live lizards would not provide the precision needed and skeletonising lizards would be extremely time consuming. Consequently, the lizards were x-rayed.

A random selection of individuals was chosen from each of the populations of the study species for osteological measurements. The lizards were killed by freezing and subsequently thawed to allow them to be positioned for x-raying. They were laid out on their ventral surface with legs outstretched from the body at 90°, with the feet placed flat and the toes straightened. The lizards were x-rayed on a mammogram machine. This allowed even the smallest and least calcified bones, such as the toes, to be seen clearly. All lizards were x-rayed alongside a small metal staple (9 mm in length) to provide a measurement scale.

The x-rays were video taped with a Sony video camera using the "negative" mode, so that the x-rays were converted to an image of black bones on a white background. The video footage of the x-rays was input into a Macintosh Performa power PC (6400/180) computer for analysis. The osteological measurements were calculated using the programme NIH. This allowed the bone lengths to be measured to ± 0.01 mm

using the metal staple on each x-ray as a scale. A number of osteological measurements were recorded for each lizard, as listed below.

1. Interlimb length (ILL) – Sum of the individual vertebral lengths between fore- and hindlimbs.
2. Humerus length (HUL), radioulna length (RUL), forefoot length (FFT). HUL and RUL were the distance from the proximal to the distal articular surface of each element of the forelimb. FFT was taken as the sum of the metacarpal and phalange lengths of the third digit.
3. Forelimb length (FL) – Sum of the lengths of the individual limb elements.
4. Femur length (FEL), tibiofibula length (TFL), hindfoot length (HFT). FEL and TFL were the distance from the proximal to the distal articular surface of each element of the hindlimb. HFT was taken as the sum of the metatarsal and phalange lengths of the third digit.
5. Hindlimb length (HL) – Sum of the lengths of all individual elements.

7.2.2 Statistical analysis

Two statistical methods were used to analyse the osteometric characters. A least-squares regression analysis was used to analyse the relationship between leg lengths and snout-vent lengths. Bone ratios were used to compare bone lengths between the species, these included:

1. HUL/FL;
2. RUL/FL;
3. FFT/FL;
4. RUL/HUL;
5. FEL/HL;
6. TFL/HL;
7. HFT/HL; and
8. HFT/FEL.

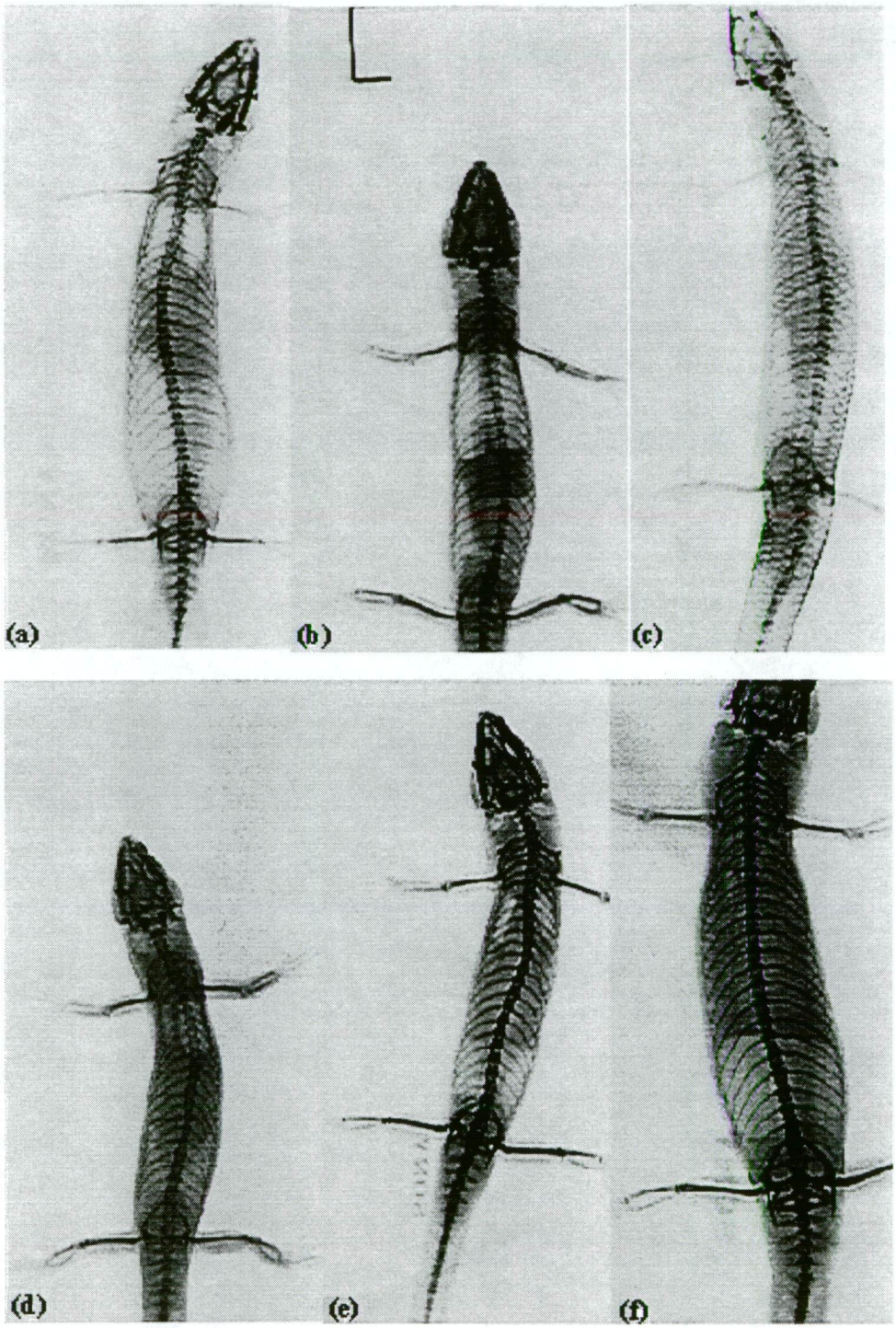


Plate 7.1 Video images of x-rays , including: (a) female *N. microlepidotus* (Mt Hartz); (b) male *N. microlepidotus* (Mt Hartz); (c) male *N. metallicus* (Clarence Lagoon); (d) male *N. pretiosus* (Pirate's Bay); (e) male *N. greeni* (Ben Lomond); and (f) female *N. ocellatus* (Orford).

Table 7.1 Osteological measurements recorded for each population of *Niveoscincus* and *Pseudemoia entrecasteauxii* (values are mean ± standard error)

	n	SVL (mm)	ILL (mm)	HUL (mm)	RUL (mm)	FFT (mm)	FL (mm)	FEL (mm)	TFL (mm)	HFT (mm)	HL (mm)
N. coventryi (Mt St Leonards)	16	43.5 ± 1.55	28.94 ± 1.027	4.36 ± 0.165	2.99 ± 0.109	4.15 ± 0.049	11.50 ± 0.303	5.77 ± 0.157	3.46 ± 0.094	6.79 ± 0.235	16.01 ± 0.475
N. greeni (Ben Lomond)	22	56.72 ± 1.57	31.37 ± 1.065	7.63 ± 0.186	5.03 ± 0.115	7.13 ± 0.128	19.78 ± 0.355	8.63 ± 0.160	5.46 ± 0.137	10.78 ± 0.130	24.87 ± 0.388
N greeni (Mt Pelion East)	16	56.0 ± 3.81	31.81 ± 2.384	7.78 ± 0.545	5.12 ± 0.332	7.30 ± 0.423	20.19 ± 1.267	8.86 ± 0.559	5.52 ± 0.321	10.83 ± 0.600	25.20 ± 1.461
N. metallicus (Orford)	26	49.8 ± 1.39	31.78 ± 0.916	5.66 ± 0.106	3.57 ± 0.118	4.49 ± 0.089	13.72 ± 0.234	6.73 ± 0.155	3.99 ± 0.087	7.94 ± 0.200	18.66 ± 0.368
N. metallicus (Clarence Lagoon)	22	54.5 ± 1.14	32.48 ± 1.029	5.98 ± 0.114	3.71 ± 0.104	5.00 ± 0.127	14.69 ± 0.299	7.17 ± 0.146	4.27 ± 0.128	8.65 ± 0.301	20.08 ± 0.472
N. microlepidotus (Mt Hartz)	24	56.4 ± 1.67	34.09 ± 1.349	6.99 ± 0.185	4.89 ± 0.178	6.43 ± 0.125	18.32 ± 0.442	8.31 ± 0.234	5.12 ± 0.140	10.14 ± 0.237	23.56 ± 0.558
N. microlepidotus (Mt Wellington)	24	56.9 ± 1.45	34.89 ± 1.094	7.26 ± 0.198	5.19 ± 0.175	6.79 ± 0.134	18.78 ± 0.385	8.81 ± 0.214	5.42 ± 0.184	10.49 ± 0248	23.95 ± 0.517
N. ocellatus (Lake Augusta)	18	71.4 ± 1.99	40.13 ± 0.853	9.09 ± 0.187	5.92 ± 0.170	8.12 ± 0.232	23.13 ± 0.532	10.27 ± 0.239	6.56 ± 0.195	12.53 ± 0.345	29.36 ± 0.710
N. ocellatus (Orford)	28	60.6 ± 0.89	33.86 ± 0.632	7.73 ± 0.110	5.03 ± 0.094	6.58 ± 0.126	19.34 ± 0.265	9.16 ± 0.106	5.61 ± 0.078	10.27 ± 0.142	25.03 ± 0.239
N. orocryptus (Mt Eliza)	24	51.7 ± 1.096	32.53 ± 0.958	6.48 ± 0.150	4.28 ± 0.102	5.90 ± 0.124	16.66 ± 0.344	7.71 ± 0.129	4.92 ± 0.203	9.11 ± 0.29	21.73 ± 0.597
N. orocryptus (Mt Hartz)	24	53.3 ± 2.26	32.49 ± 1.596	6.55 ± 0.184	4.27 ± 0.148	5.81 ± 0.185	16.64 ± 0.47	7.64 ± 0.204	4.69 ± 0.130	9.55 ± 0.221	21.88 ± 0.491
N. pretiosus (Clarence Lagoon)	12	48.5 ± 1.06	29.65 ± 1.043	6.13 ± 0.149	4.04 ± 0.076	5.72 ± 0.179	15.88 ± 0.379	7.36 ± 0.204	4.39 ± 0.141	8.38 ± 0.315	20.13 ± 0.605
N. pretiosus (Pirates Bay)	12	48.9 ± 1.56	29.91 ± 1.451	6.38 ± 0.148	4.26 ± 0.108	5.99 ± 0.178	16.08 ± 0.315	7.52 ± 0.194	4.64 ± 0.270	8.59 ± 0.267	20.46 ± 0.489
P. entrecasteauxii (Hobart)	16	46.7 ± 1.60	28.15 ± 0.983	3.99 ± 0.176	2.61 ± 0.128	3.94 ± 0.045	10.54 ± 0.321	5.58 ± 0.137	3.25 ± 0.065	6.42 ± 0.233	15.25 ± 0.423

7.3.3 Forelimb morphology

The total forelimb length varied significantly between the species examined ($F_{8,244}$ = 105.19; $p < 0.001$). The species with the longest front leg length was *N. ocellatus* (Lake Augusta), while that with the shortest was *Pseudemoia entrecasteauxii* (Table 7.1). The species of *Niveoscincus* with the shortest forelimb length was *N. coventryi*. When the species were grouped according to ecomorph type (ground-dwelling: *N. metallicus, N. coventryi, P. entrecasteauxii*; arboreal: *N. pretiosus, N. orocryptus* (Mt Eliza); and saxicolous: *N. greeni, N. ocellatus, N. microlepidotus, N. orocryptus* (Mt Hartz)), there was a significant difference in forelimb length ($F_{2,251}$ = 221.09; $p < 0.001$). There was also a significant difference between the populations of *N. ocellatus* ($F_{1,44}$ = 104.84; $p < 0.001$) and *N. metallicus* ($F_{1,46}$ = 14.08; $p < 0.001$).

The total forelimb length was significantly related to the snout-vent length when data for all species were combined ($p < 0.001$), with leg length increasing as snout-vent length increased (Figure 7.1). Consequently, a regression analysis was applied to the data before forelimb length was included in the comparative analysis in Chapter 8.

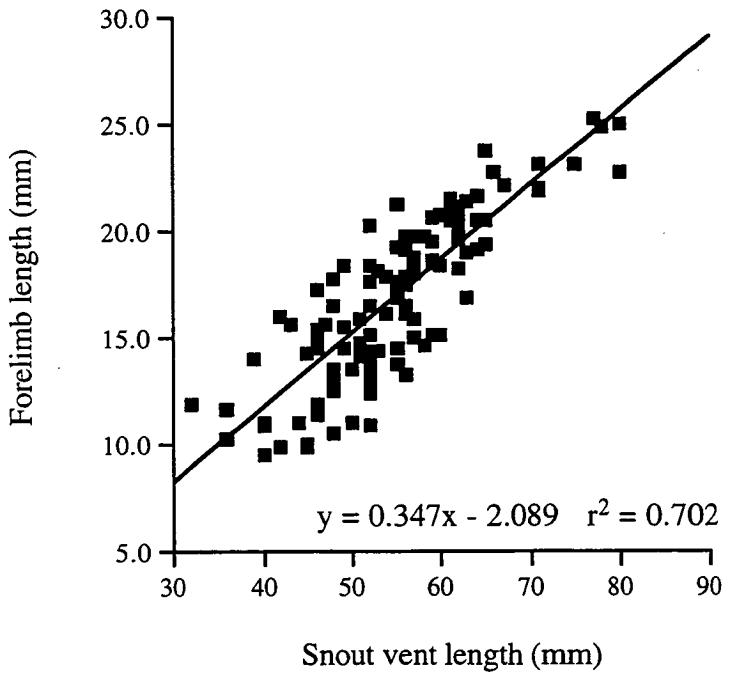


Figure 7.1 A least squares linear regression of front leg length vs snout-vent length in all species studied.

Forelimb ratios

The proportional length of the humerus (HUL/FL) was greatest in *N. metallicus* and that of the radioulna (RUL/FL) was greatest in *N. microlepidotus* (Table 7.2). The proportional length of the humerus (HUL/FL) differed significantly between the species ($F_{8,275} = 25.63$; $p < 0.001$). A Fisher's LSD *post hoc* test indicated that *N. metallicus* was significantly different from all other species ($p < 0.001$). The relative lengths of the radioulna (RUL/FL) did not differ between the species. The proportional length of the forefoot (FFT/FL) was greatest in *P. entrecasteauxii*. There was a significant difference between the species in the relative length of the forefoot (FFT/FL) ($F_{8,275} = 18.55$; $p < 0.001$). A Fisher's LSD posthoc test indicated that *N. metallicus* was significantly different from all other species while *P. entrecasteauxii* differed significantly from all *Niveoscincus* species except *N. coventryi.* The ratio between humerus and forefoot (FFT/HUL) was greatest in *N. greeni.* The ratio of the humerus to forefoot (FFT/HUL) differed significantly between the species ($F_{8,275} = 26.296$; $p < 0.001$). A Fisher's LSD *post hoc* test indicated that *N. metallicus* differed significantly from all other species and *N. greeni* differed significantly from all species except *N. pretiosus.* There were no significant differences between the populations of each species.

There was a significant difference in the proportional lengths of the humerus (HUL/FL) ($F_{2,281} = 9.08$; $p < 0.001$) when the species were grouped according to ecomorph type. There was also a significant difference between the species in the relationship between humerus and forefoot (FFT/HUL) ($F_{8,281} = 5.40$; $p = 0.005$). A Fisher's LSD *post hoc* test indicated that the ground-dwelling species differed significantly from both the saxicolous ($p = 0.002$) and the arboreal species ($p = 0.001$). However, there was no significant difference between the saxicolous and arboreal species. There were also no significant inter-populational differences in the proportional lengths of the forelimb measurements in *Niveoscincus*.

Table 7.2 Proportions of the forelimb for each population of *Niveoscincus* and *Pseudemoia entrecasteauxii* (mean, range and standard error are provided)

		HUL/FL			RUL/FL			FFT/FL			FFT/HUL		
	n	mean	range	s.e.	mean	range	s.e.	mean	range	s.e.	mean	range	s.e.
N. coventryi (Mt St Leonards)	16	0.38	0.37 - 0.41	0.006	0.26	0.23 - 0.27	0.005	0.34	0.34 - 0.38	0.005	0.86	0.82 - 0.96	0.015
N. greeni (Ben Lomond)	22	0.39	0.36 - 0.49	0.004	0.25	0.24 - 0.28	0.003	0.36	0.34 - 0.29	0.005	0.94	0.83 - 1.09	0.022
N. greeni (Mt Pelion East)	16	0.38	0.37 - 0.41	0.005	0.25	0.24 - 0.26	0.004	0.36	0.34 -0.38	0.006	0.95	0.83 - 1.04	0.027
N. metallicus (Orford)	26	0.41	0.39 - 0.43	0.004	0.26	0.21 - 0.29	0.006	0.33	0.29 - 0.37	0.006	0.84	0.78 - 0.95	0.013
N. metallicus (Clarence Lagoon)	22	0.41	0.39 - 0.42	0.002	0.25	0.23 - 0.28	0.004	0.34	0.32 - 0.38	0.005	0.80	0.69 - 0.89	0.018
N. microlepidotus (Mt Hartz)	24	0.38	0.36 - 0.41	0.004	0.27	0.25 - 0.31	0.004	0.35	0.33 - 0.37	0.004	0.92	0.83 - 1.03	0.016
N. microlepidotus (Mt Wellington)	24	0.38	0.37 - 0.41	0.004	0.26	0.25 - 0.31	0.004	0.35	0.33 - 0.38	0.003	0.92	0.83 - 1.01	0.017
N. ocellatus (Lake Augusta)	18	0.39	0.38 - 0.40	0.004	0.26	0.24 - 0.27	0.004	0.35	0.34 - 0.38	0.004	0.89	0.84 - 0.98	0.017
N. ocellatus (Orford)	28	0.40	0.38 - 0.44	0.004	0.26	0.24 - 0.28	0.003	0.34	0.32 - 0.36	0.004	0.85	0.76 - 0.95	0.016
N. orocryptus (Mt Eliza)	24	0.39	0.38 - 0.40	0.002	0.26	0.24 - 0.27	0.003	0.35	0.33 - 0.37	0.003	0.91	0.83 - 0.96	0.012
N. orocryptus (Mt Hartz)	24	0.39	0.37 - 0.41	0.004	0.26	0.24 - 0.28	0.004	0.35	0.33 - 0.37	0.004	0.89	0.82 - 0.98	0.018
N. pretiosus (Clarence Lagoon)	12	0.39	0.38 - 0.39	0.003	0.25	0.24 - 0.27	0.004	0.36	0.35 - 0.37	0.003	0.93	0.91 - 0.96	0.008
N. pretiosus (Pirates Bay)	12	0.39	0.36 - 0.39	0.004	0.25	0.24 - 0.27	0.004	0.35	0.33 - 0.37	0.004	0.93	0.90 - 0.96	0.009
P. entrecasteauxii (Hobart)	16	0.38	0.36 - 0.41	0.007	0.25	0.22 - 0.27	0.006	0.34	0.33-0.39	0.008	0.86	0.82 - 0.96	0.015

7.3.4 Hindlimb morphology

Total hindlimb length (HL) varied significantly between the species ($F_{9,244} = 81.00$; $p < 0.001$). The species with longest rear leg length was *N. ocellatus* (Lake Augusta), while that with the shortest was found to be *Pseudemoia entrecasteauxii* (Table 7.1). The species of *Niveoscincus* with the shortest hindlimb length was *N. coventryi*. When the species were grouped according to ecomorph type (ground-dwelling: *N. metallicus, N. coventryi, P. entrecasteauxii*; arboreal: *N. pretiosus, N. orocryptus* (Mt Eliza); and saxicolous: *N. greeni, N. ocellatus, N. microlepidotus, N. orocryptus* (Mt Hartz)), there was also a significant difference in rear leg length ($F_{2,251} = 176.69$; $p < 0.001$). There was a significant difference between the populations of both *N. ocellatus* ($F_{1,44} = 96.46$; $p < 0.001$) and *N. metallicus* ($F_{1,46} = 12.14$; $p = 0.001$).

When all data were combined the total hindlimb length was found to be significantly related to snout-vent length ($p < 0.001$) (Figure 7.2); leg length increased with snout-vent length. Consequently, regression analysis was applied to the data before hindlimb length was included in the comparative analysis in Chapter 8.

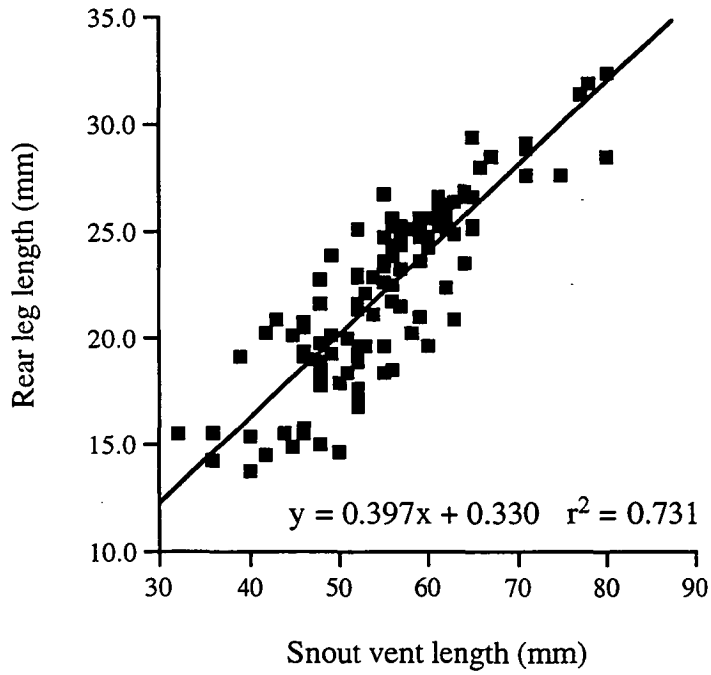


Figure 7.2 A least squares linear regression of rear leg length vs snout-vent length in all species studied.

Hindlimb ratios

The proportional length of the femur (FEL/HL) was found to be greatest in *N. ocellatus* (Orford), *N. pretiosus* and *P. entrecasteauxii* and that for the tibiofibula (TFL/HL) was greatest in *N. orocryptus* (Mt Hartz) (Table 7.3). There was a significant difference between the species in the proportional lengths of the femur (FEL/HL) ($F_{8,275} = 5.50$; $p < 0.001$). A Fisher's LSD *post hoc* test indicated that *N. greeni* differed significantly from all species except *N. microlepidotus* and *N. orocryptus* (Mt Hartz). There was a significant difference between the species in the proportional length of the tibiofibula (TFL/HL) ($F_{8,275} = 6.71$; $p < 0.001$). A Fisher's LSD *post hoc* test indicated that *N. greeni* differed significantly from all species except *N. microlepidotus*, *N. pretiosus* and *N. orocryptus* (Mt Hartz). The proportional length of the hindfoot (HFT/HL) was greatest in *N. orocryptus* (Mt Hartz). There was a significant difference between the species in the proportional length of the hindfoot (HFT/HL) ($F_{8,275} = 8.34$; $p < 0.001$). A Fisher's LSD *post hoc* test indicated that *N. greeni* differed significantly from all species except *N. microlepidotus* and *N. orocryptus* (Mt Hartz). The ratio of hindfoot to femur length (HFL/FEL) was greatest in *N. greeni* and *N. orocryptus* (Mt Hartz). There was a significant difference between the species in the relationship between hindfoot and femur length (HFL/FEL) ($F_{8,275} = 6.79$; $p < 0.001$). A Fisher's LSD *post hoc* test indicated that *N. greeni* differed significantly from all species except *N. microlepidotus* and *N. orocryptus* (Mt Hartz).

When the species were grouped according to ecomorph type there was a significant difference in the proportional lengths of the femur (FEL/HL) ($F_{2,281} = 9.79$; $p < 0.001$), tibiofibula (TFL/HL) ($F_{2,281} = 12.43$; $p < 0.001$) and the hindfoot (HFL/HL) ($F_{2,281} = 8.73$; $p < 0.001$). There was also a significant difference between the species in the relationship between hindfoot and femur length (HFL/FEL) ($F_{2,281} = 8.77$; $p < 0.001$). The saxicolous species were significantly different from both the ground-dwelling (Fisher's LSD *post hoc* test $p = 0.007$) and the arboreal species ($p < 0.001$). However, there was no significant difference between the ground-dwelling and arboreal species.

Table 7.3 Proportions of the hindlimb for each population of *Niveoscincus* and *Pseudemoia entrecasteauxii* (mean, range and standard error are provided)

		FEL/HL			TFL/HL			HFT/HL			HFT/FEL		
	n	mean	range	s.e.	mean	range	s.e.	mean	range	s.e.	mean	range	s.e.
N. coventryi (Mt St Leonards)	16	0.36	0.36 - 0.37	0.002	0.22	0.21 - 0.22	0.002	0.42	0.41 - 0.44	0.003	1.17	1.09 - 1.23	0.015
N. greeni (Ben Lomond)	22	0.35	0.33 - 0.36	0.003	0.22	0.20 - 0.24	0.003	0.43	0.42 - 0.45	0.003	1.25	1.16 - 1.35	0.016
N. greeni (Mt Pelion East)	16	0.35	0.33 - 0.36	0.004	0.22	0.21 - 0.23	0.002	0.43	0.42 - 0.44	0.003	1.23	1.16 - 1.33	0.024
N. metallicus (Orford)	26	0.36	0.33 - 0.39	0.005	0.21	0.19 - 0.23	0.004	0.43	0.39 - 0.45	0.005	1.18	0.98 - 1.47	0.045
N. metallicus (Clarence Lagoon)	22	0.36	0.31 - 0.39	0.007	0.21	0.19 - 0.23	0.003	0.43	0.39 - 0.47	0.007	1.18	1.00 - 1.31	0.027
N. microlepidotus (Mt Hartz)	24	0.35	0.33 - 0.37	0.004	0.22	0.19 - 0.24	0.003	0.43	0.41 - 0.46	0.004	1.22	1.11 - 1.38	0.022
N. microlepidotus (Mt Wellington)	24	0.35	0.33 - 0.39	0.005	0.22	0.19 - 0.23	0.003	0.43	0.41 - 0.47	0.004	1.22	1.11 - 1.38	0.022
N. ocellatus (Lake Augusta)	18	0.35	0.33 - 0.37	0.004	0.22	0.21 - 0.23	0.002	0.43	0.40 - 0.46	0.005	1.22	1.09 - 1.38	0.028
N. ocellatus (Orford)	28	0.37	0.35 - 0.39	0.003	0.22	0.21 - 0.24	0.002	0.41	0.39 - 0.43	0.003	1.12	1.01 - 1.22	0.028
N. orocryptus (Mt Eliza).	24	0.36	0.33 - 0.39	0.005	0.22	0.19 - 0.23	0.003	0.42	0.39 - 0.43	0.003	1.18	1.01 - 1.30	0.023
N. orocryptus (Mt Hartz)	24	0.35	0.33 - 0.38	0.004	0.23	0.21 - 0.25	0.004	0.44	0.40 - 0.46	0.005	1.26	1.09 - 1.40	0.028
N. pretiosus (Clarence Lagoon)	12	0.37	0.35 - 0.39	0.006	0.22	0.21 - 0.23	0.003	0.42	0.39 - 0.43	0.004	1.13	1.01 - 1.22	0.030
N. pretiosus (Pirates Bay)	12	0.37	0.35 - 0.38	0.005	0.22	0.21 - 0.24	0.002	0.42	0.39 - 0.43	0.003	1.13	1.01 - 1.22	0.028
P. entrecasteauxii (Hobart)	16	0.37	0.36 - 0.39	0.004	0.21	0.20 - 0.22	0.002	0.42	0.39 - 0.43	0.004	1.15	1.02 - 1.21	0.023

A significant difference between the populations of *N. ocellatus* was found for the proportional lengths of the femur (FEL/HL) ($F_{1,21} = 9.21$; $p = 0.006$), the hindfoot (HFT/HL) ($F_{1,21} = 7.94$; $p = 0.010$), and in the relationship between hindfoot and femur length (HFL/FEL) ($F_{1,21} = 9.60$; $p = 0.005$). No other significant inter-populational differences were found.

7.4 Discussion

7.4.1 Osteological characters

Many evolutionary studies have been conducted from the morphological perspective (eg. Liem, 1973; Alberch, 1980; Livesay and Humphrey, 1986; Schaefer and Lauder, 1986; Livesey, 1989). In such studies morphology is commonly interpreted in terms of behaviour, adjustment to the external environment and functional morphology (Hildebrand, 1995). Functional morphology is an area of research which has the potential to provide insight into the dynamic nature of morphology and its phylogenetic development. A number of these studies have considered the contribution of various appendicular skeletal elements to the sprawling locomotion found in reptiles and amphibians, with particular emphasis on the pelvic girdle and hindlimb morphology (eg. Brinkman, 1980, 1981; Rewcastle, 1980, 1983; Peterson, 1984; Hildebrand, 1985; Ashley-Ross, 1994a,b).

All of the *Niveoscincus* species examined in my study have a typically reptilian, sprawling gait. Nonetheless, distinct differences occured in movement techniques employed between the ecomorph types (arboreal, saxicolous and ground-dwelling) (see Chapter 6). My study has indicated that there are also subtle morphological differences, both between species and ecomorph types in *Niveoscincus*. Variation in limb length is often correlated with behaviour and ecology in lizards (Losos and Sinervo, 1989). For example, in the deserts of western Australia, long-legged skinks of

the genus *Ctenotus* tend to utilise open spaces, while shorter-legged species move within dense vegetation (Pianka, 1969). Anolids also have a wide range of body forms and species occupying similar microhabitats had convergent morphology, in traits such as lamellae number, tail length, and fore- and hindlimb length (Losos, 1990a). Losos and Sinervo (1989) reported that leg length in anolids is related to the perch size used, with the short-legged *Anolis valencienni* uses the very narrow perches. The species of *Niveoscincus* vary in external morphological characteristics, some, such as the ground-dwelling species *N. metallicus,* having a relatively long flattened bodyform, while others, such as the arboreal species *N. pretiosus,* possess a short and narrow body form. This section will discuss the morphological variation recorded in *Niveoscincus* in terms of the relationship between body shape and ecomorph type. A more detailed discussion of the evolutionary significance of morphology, locomotion and ecology in *Niveoscincus* can be found in Chapter 8.

Saxicolous species

It was shown in Chapter 6 that the strong jumpers, *N. greeni*, *N. ocellatus*, *N. orocryptus* (Mt Hartz) and *N. microlepidotus*, tend to land front feet first. Consequently, the forelimbs absorb the initial landing force. The strong jumping species, such as *N. greeni,* have a relatively short ilium but long feet. This arrangement may reflect a need for shorter but heavier ilia to absorb the shock of landing and a requirement for large feet to spread the touch-down force over the maximum area. The stronger jumpers also have long hindlimbs, which may provide greater jumping ability, since these limbs provide the propulsive force in jumping.

Ground-dwelling species

The ground-dwelling species, *N. metallicus, N. coventryi,* and *P. entrecasteauxii*, spend much of their time moving through undergrowth such as grass and litter layers. The skinks forage in this litter, flee into it and shelter in the litter/soil interface during bad weather (Greer, 1989). An association with this microhabitat may have led to changes in habit (ie., more cryptozoic and/or nocturnal behaviour) and morphology (ie., body

elongation and limb reduction). Locomotion through a microhabitat such as this may be most efficient if sinusoidal body movements are used rather than propulsion from the legs. Long legs may in fact hinder locomotion in dense vegetation. These ground-dwelling species all have short legs and long slender bodies. This may provide an advantage in moving through their microhabitat, but it should also be noted that *N. metallicus* has a longer humerus in proportion to the front leg than all the other *Niveoscincus* species studied.

The relatively long humerus in *N. metallicus* may allow a greater musculature and strength in the forelimb that enhances the ability to manoeuvre through litter and dense vegetation. The elongation of front limbs in comparison to rear legs has been observed in a number of Australian skinks, such as in the genus of *Anomalopus*. Gans (1985) reported that *Anomalopus* species only use lateral undulations of the body during high velocity movement; at slower speeds they propel themselves by a limbed concertina motion. The forelimbs "walk" the head and neck around minor obstructions in the heterogenous soil they inhabit. The technique that *N. metallicus* employs when moving through dense vegetation has not been studied, but it is possible that the forelimbs play a significant role.

Arboreal species

Arboreal lizards are often distinguished from terrestrial species by the presence of adhesive or prehensile organs, body shapes and behaviours which are specifically adaptive for arboreal habitats (Peterson, 1984). The assemblage of arboreal lizards includes some highly specialised genera (eg. *Draco* and *Gekko*) and displays a tremendous diversity of evolutionary and ecological patterns. Evolutionary patterns range from isolated arboreal species within terrestrial or semi-fossorial groups to large adaptive radiations, as occurs in *Chamaeleo*.

The arboreal species of *Niveoscincus* are small agile lizards with short bodies, legs of a moderate length and large feet. Thus, *Niveoscincus pretiosus* and *N. orocryptus* (Mt

Eliza) are characterised by short bodies, relatively long femurs and front feet, all of which may assist in climbing. A short body may reduce the instability associated with lateral movement of the trunk seen in the ground-dwelling species such as *N. metallicus* when climbing. It was reported in Chapter 6 that the ground-dwelling species, such as *N. metallicus*, had difficulty in moving on the narrow climbing rods used to test climbing because the lateral movements of their body appeared to create balance problems. The large frontfeet would also enhance reach, stability and gripping while climbing on a discontinuous and three-dimensional substrate. Similarly, the relatively long femur found in the arboreal species of *Niveoscincus* would allow greater strength in the hindlimb for balancing, bracing and propulsion on narrow and unstable surfaces.

7.4.2 Cursoriality

Cursoriality implies swiftness or ease of running. Cursorial adaptations include the lengthening of the distal limb segments, the reduction, compression or loss of lateral metapodials and phalanges (and also of the ulna and fibula) and a change in the foot stance from the primitive plantigrade to digitigrade or unguligrade (Hildebrand, 1985). Consequently, functional morphologists have often used the metatarsal/femur ratio as an indicator of cursoriality in mammals (Garland and Janis, 1993). This ratio reflects the degree to which distal elements of the hindlimb are elongated relative to the proximal elements. Larger values indicate increased cursoriality and enhanced locomotor performance. Metatarsal/femur ratios have been found to be a significant predictor of running speed within a combined sample of 19 species of Carnivora and 30 ungulates (Garland and Janis, 1993). However, even though cursorial lizards have relatively long legs, their limb proportions do not generally follow the rule of an increase in the relative length of the tibia, metacarpals and/or metatarsals (Hildebrand, 1995).

A positive relationship between size-corrected hindlimb length and maximal running speed exists in some species of lizards (Losos, 1990). The hindlimb is elongated in lizards capable of rapid locomotor gaits, particularly in bipedal gaits such as observed

in the genus *Basiliscus* (Laerm, 1974). Lengthening of the hindlimb is a cursorial adaptation that permits a longer stride. This has involved each limb segment in bipedal iguanids such as *Basiliscus*. A larger projected surface area of the foot is provided by long flattened toes, allowing a greater propulsive force in bipedal locomotion.

The current study examined the hindfoot/femur (HFT/FEL) ratio in *Niveoscincus*. It found that the faster running species, such as *N. greeni, N. ocellatus* (Lake Augusta) and *N. orocryptus* (Mt Hartz), all had high HFT/FEL values. This suggests that HFT/FEL predicts maximal running speed in *Niveoscincus*. The increase in the hindlimb length of the fast running species *N. greeni* appears to have occurred mainly in the length of the foot. This would increase the propulsive force in both running and jumping which are the common locomotory modes in the saxicolous species of *Niveoscincus*. However, other factors apart from leg length may also account for the fast maximal running speed in saxicolous *Niveoscincus* species. Variation in muscle masses or physiology or in limb postures may also be of great importance (Garland and Janis, 1993) but these were outside the scope of this study.

CHAPTER EIGHT

COMPARATIVE ANALYSIS OF MICROHABITAT, BEHAVIOURAL, PERFORMANCE AND MORPHOLOGICAL COVARIATION

8.1 Introduction

8.1.1 The comparative method

Fossil records provide the only direct evidence of past changes (Martins and Garland, 1991). Despite this, attempts to reconstruct the evolutionary history of the characteristics of an organism based, primarily or exclusively, on neontological data are common. This is particularly true for some traits, such as behavioural and physiological characters, for which palaeontological evidence is rarely available (Martins and Garland, 1991). It is often a goal of such work to infer the state of a trait in an ancestral form, generally based on some sort of parsimony argument. Alternatively, the disribution of a trait may be examined in relation to ecological or environmental characteristics (Huey, 1987). Relationships identified by such comparisons may be used to formulate hypotheses about adaptation or to test pre-existing hypotheses.

In recent decades the comparative method has undergone a renaissance in evolutionary biology as researchers develop new ways to incorporate taxonomic and phylogenetic information into the design and analysis of interspecific data (see Martins and Hansen, 1996). Phylogenies and new phylogenetic comparative methods allow researchers to infer the patterns and processes of character evolution from the patterns observed in data measured from extant species.

The evolution of particular combinations of distinct phenotypic traits in response to natural selection (co-adaptation) is based on the notion that it is the interaction among

traits that determines performance and hence fitness (Bauwens *et al.*, 1995). This paradigm may be substantiated by observations of the correlated evolution of traits at distinct levels of biological organisation (eg morphology, physiology, performance and behaviour). These factors were included in the paradigm illustrated in Chapter 5 which was an expansion of that provided by Arnold (1983). The relationship between these factors is straightforward and logical but not necessarily complete (Garland and Losos, 1994). For example, habitat is another important factor which may influence behaviour, performance and morphology (Figure 8.1). Thus, selection for high sprint speed is likely to have been most intense in species that live in habitats that are sparsely vegetated, exhibit high densities of (specialised) predators, and/or contain profitable prey types that are fast moving (Bauwens *et al.*, 1995). Intense selection for increased sprinting ability should result in the evolution of those morphological (long hind limbs relative to body length) and physiological (a high optimum temperature for sprinting) traits that allow lizards to achieve high maximum speeds.

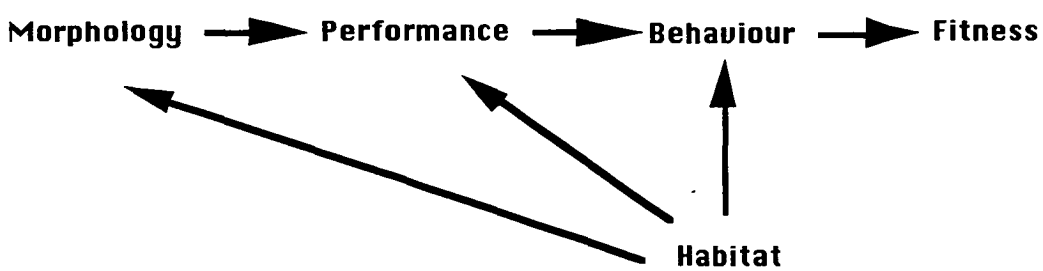


Figure 8.1 Inclusion of some factors which would affect Arnold's (1983) paradigm, taken from Garland and Losos (1994). Habitat may affect basic physiological and biochemical properties as well as behaviour, performance and morphology.

This paradigm can be used to understand or predict a relationship between morphology and habitat use among populations or species (Garland and Losos, 1994). Morphological differences among individuals of a population may lead to differences in performance abilities, which will in turn affect fitness. Consequently, the most "fit" morphology should evolve within a population, assuming there are no constraints on the evolutionary process. Similarly, natural selection will favour the evolution of morphologies most appropriate for a specific habitat.

This chapter addresses a number of important issues in ecomorphology. A tight relationship between performance and morphology is an important assumption of ecomorphological hypotheses (Bauwens *et al.*, 1995). However, it has been assumed in many studies that if a species is a fast runner it will have high performance abilities in other tasks. It has been a central tenet of evolutionary biology that specialisation for one task curtails the ability to perform a wide variety of tasks. This is the "jack of all trades, master of none" theory (Huey and Hertz, 1984). This chapter will cover these issues, as listed below:

(1) the interspecific relationships between morphology and a number of performance traits in *Niveoscincus* are quantified;
(2) the possible trade-offs between different modes of locomotion are examined; and
(3) the co- evolution of performance, morphology, behaviour, and microhabitat occupation is considered, together with a discussion of how these parameters may affect the fitness of a lizard in its environment.

8.1.2 Phylogenetic analyses

Traditional comparative studies examine evolutionary associations of traits by comparing different species, regardless of their phylogenetic relationships (Garland *et al.*, 1991). Typically, species are compared and patterns defined by the existence of statistically significant relationships between traits. However, standard statistical techniques are inappropriate for comparative analyses as they do not address the problem of statistical dependence. Data for related species are not independent because organisms descend in a hierarchical fashion from common ancestors (Felsenstein, 1985). This is the "degrees of freedom" or "effective sample size" problem that has been mentioned frequently in the recent evolutionary literature (see Martins and Hansen, 1996). The effective sample size of measured data depends on the number of independent data points rather than the number of samples taken.

A number of quantitative methods for inferring relationships between traits while taking into account phylogeny have been proposed (see Martins and Garland, 1991; Garland *et al.*, 1993; Martins and Hansen, 1996). It is statistically unacceptable not to take phylogeny into account (Garland *et al.*, 1993). Computer simulations have shown that standard statistical analyses which ignore phylogeny entirely (eg TIPS) yield inflated Type I error rates, have a low power, and produce relatively inaccurate estimates of evolutionary correlations (Martins and Garland, 1991).

Independent contrasts

There are several methods that can be grouped under the broad category of independent contrasts, which originated with the analytical procedure proposed by Felsenstein (1985). This procedure was originally devised as a way of addressing the problem of statistical dependence of comparative data within a population-genetics framework (Martins and Hansen, 1996). Felsenstein's (1985) phylogenetically independent contrasts is probably the most frequently used of the methods available for analysis with any phylogenetic tree (including soft (reflecting uncertainty) and hard polytomies) and various branch lengths (Diaz-Uriate and Garland, 1996). Under this model, although species data are not independent, the differences or contrasts between certain pairs of species on the phylogeny are independent of one another (Figure 8.2)

Felsenstein's (1985) original method assumes: (1) that within-species variation does not exist or is negligible; (2) a correct topology; (3) branch lengths measured in units of expected variance of character evolution; and (4) a Brownian motion (BM) model of character evolution. These assumptions allow the computation of phylogenetically independent contrasts that can be used both for statistical estimation and hypothesis testing. Independent contrasts yield the nominal type I error rates (probability of rejecting the null hypothesis when it is true) for testing the significance of correlations and regressions, when these assumptions are not violated. Type I error rates may deviate from nominal values if the assumptions are violated (Diaz-Uriate and Garland,

1996). Inflated type I error rates seriously affect hypothesis testing and lead to the rejection of the null hypothesis more frequently than specified by nominal P values.

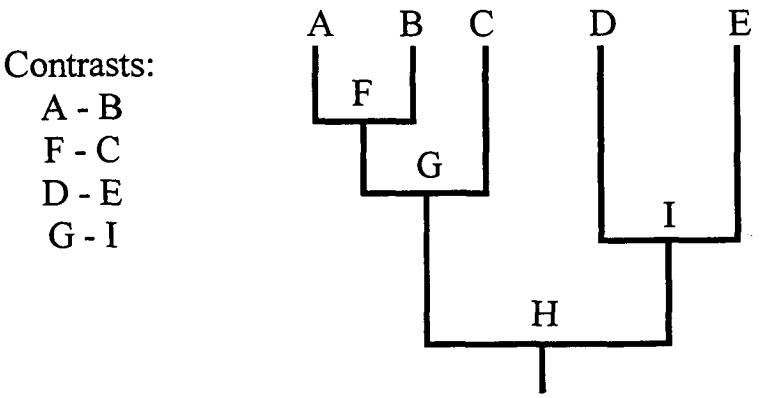


Figure 8.2 Illustration of Felsenstein's (1985) method of independent contrasts, taken from Martins and Hansen (1996). Even though the measured species (A through to E) are not statistically independent of one another, under a Brownian motion model of phenotypic evolution certain "contrasts" between pairs of taxa are independent. Felsenstein's (1985) method consists of a numerical algorithm for calculating *N*-1 of these contrasts (where *N* is the number of measured species) and then standardising them appropriately, so that they can be used in any standard statistics.

The Brownian Motion (BM) model is a good approximation of evolution by purely random genetic drift with no selection but may also be appropriate for some types of selection, such as that caused by randomly fluctuating environmental conditions. The model is very simple and is probably unrealistic in evolutionary processes (Diaz-Uriate and Garland, 1996). However, it does not mean that independent contrasts cannot profitably be applied to real data. The key issue is the robustness of the independent contrasts method when the BM model is incorrect and/or the available branch lengths are not reasonable surrogates for expected variance of character change.

Diaz-Uriate and Garland (1996) used computer simulations of character evolution on specified phylogenetic trees to address the effects of deviations from the BM model on the performance of independent contrasts for testing hypotheses about correlated evolution. The evolutionary models used ranged from slight deviations from BM (eg Ornstein-Uhlenbeck model with a moderate amount of stabilising selection) to extreme deviations (eg punctuated equilibrium, in which character evolution can occur in only

one daughter at each cladogenic event). They analysed the performance of each method with regard to hypothesis testing by calculating its type I error rate, as this is the aspect of statistical performance that is usually of primary concern in comparative studies. Independent contrasts yield inflated type I error rates under most of the 14 models studied that varied from BM. However, not all deviations from BM lead to inflated type I error rates. For example, simply imposing a trend on BM (shifting the mean) did not lead to inflated type I error rates. In addition, preliminary studies showed that weak limits, or weak Ornstein-Uhlenbeck decay constants had little or no effect on type I error rates. Diaz-Uriate and Garland (1996) concluded that independent contrasts is still able to provide meaningful statistical estimation and hypothesis testing.

Checking and transforming the branch lengths of a phylogeny, as suggested by Garland *et al.* (1991, 1992), almost always yields improved type I error rates with independent contrasts (Diaz-Uriate and Garland, 1996). The transformation of branch lengths is unnecessary when the BM model applies. This would lead to a loss of statistical power if one degree of freedom were subtracted for each branch length transform applied, particularly for a small number of species. One strategy is to transform branch lengths only when the need is obvious, eg when the diagnostic used shows a statistically significant pattern (Garland *et al.*, 1992).

Performance of Independent Contrasts with Small Phylogenies

It has been suggested that the independent contrasts methodology performs poorly with small phylogenies (Gittleman and Luh, 1992). The autocorrelation method was proposed as a better performer for small numbers of species. However, Purvis and Garland (1993) argued that this conclusion was misleading as polytomies were not dealt with correctly when applying independent contrasts, thus reducing the number of contrasts used. In fact, other simulations have shown that independent contrasts actually perform far better than the autocorrelation method when 15 species are involved (Bauwens *et al.*, 1995).

Removing the effects of body size

Problems may occur with the analysis of two traits that are strongly correlated with a third. Obvious examples include such characters as brain size or metabolic rate, which scale allometrically with body mass. A common approach is to regress both characters on body mass, compute residuals, then look for correlations between these residuals (Purvis and Garland, 1993). Such residuals may be analysed by techniques that take phylogeny into account. However, phylogeny should be taken into account during the creation of residuals. It is possible to use Felsenstein's method to compute standardised independent contrasts for metabolic rate, brain size and body size. Alternatively, a minimum evolution method might be used to compute inferred changes for these traits along a phylogeny (eg, Losos, 1990). These independent contrasts or inferred changes can then be used to compute separate regressions of metabolic rate on body size and of brain size on body size. Residuals from these regressions should be free of the confounding effects of body size and phylogeny, and may then be tested for correlation using standard preceedures or by reference to computer-simulated null distributions.

Population or species comparisons

It is most common to study phylogenies and morphological, performance and behavioural data for species rather than populations (Garland and Losos, 1994). However, populations can also be studied with independent contrasts and may provide essential insight into evolutionary processes (Garland and Adolph, 1991). Most interpopulational studies have been based on morphometric, allozymic or mitochondrial DNA characters (eg. Joseph *et al.*, 1995).

Complications may arise in estimating branch lengths in populations where interpopulational gene flow is common (Garland *et al.*, 1992). It has been suggested that gene flow between two diverging sister populations (ie. the members of one independent contrast) can be modeled simply by shortening branch lengths since their

divergence (Garland *et al.*, 1992). Consequently, a comparative study, such as mine, which involves two populations from each of several species provides no unusual analytical problems and could provide more information than an interspecific comparison. Contrasts of conspecific populations can provide information on microevolutionary processes, while the contrasts involving their nodes and those deeper in the tree will reflect macroevolutionary phenomena (Garland *et al.*, 1992). However, the use of more than two populations of a species in a comparative analysis would complicate findings (Garland *et al.*, 1992) because gene flow between non-sister populations would result in non independence of otherwise independent contrasts (Felsenstein, 1982).

8.1.3 A comparative analysis of morphology, performance, behaviour and habitat in *Niveoscincus*

Numerous comparative ecological studies have been conducted on Australian lizards (eg. Pianka and Pianka, 1976; James and Shine, 1985; Shine, 1986; James, 1991a,b,c). Pianka (1994) reported on the comparative ecology of *Varanus* in the Great Victorian Desert, including data on anatomy, microhabitat, activity patterns and behaviour. However, these studies have not used a statistically based comparative method which takes phylogeny into account. Only a few phylogenetic comparative studies have been conducted on Australian lizards (Garland *et al.*, 1991; Pianka, 1997). Garland *et al.* (1991) reanalysed the coadaptation of thermal physiology in 12 species of Australian skinks, including *Pseudemoia entrecasteauxii*. They found that there was no significant relationship between preferred body temperature (T_p) and the optimal body temperature for performance (T_o) or between T_o and critical thermal maxima (CTMax). However, they did find a strong positive correlation between (T_p) and CTMax.

This chapter provides possibly the first phylogenetic comparative analysis in Australia which seeks to determine whether evolution in limb morphology has been associated with evolution in locomotor mode and behaviour. The relationship between these variables and microhabitat occupation is also assessed.

Evolutionary changes in morphological traits within *Niveoscincus* (hindlimb, forelimb and snout-vent lengths), locomotory behaviour in the field and microhabitat occupation in relation to locomotory performance (maximum sprint speed, jump distance and climb speed) are also explored. Simple biomechanical models were tested to determine if there is a mechanistic relationship between, for example, maximum sprint speed and leg length. This also allows the possibility of evolutionary trade-offs between performance traits to be examined.

8.2 Materials and Methods

As has been discussed, traditional statistical procedures are usually invalid because hierarchical phylogenetic relationships of species imply that the phenotypes of different species cannot be considered as independent data points (Felsenstein, 1985, 1988). Consequently phylogenetic independent contrasts was used to test correlated evolutionary changes between pairs of phenotypic traits. The statistical package developed by Purvis and Rambaut (1995), Comparative Analysis by Independent Contrasts (CAIC), was used for the statistical analyses in this chapter.

The data used in this chapter are gained from Chapters 3, 4, 5, 6 and 7. The phylogeny and branch lengths used in the phylogenetic analysis are illustrated in Figure 8.3. These branch lengths were available for this analysis as the phylogeny is based on DNA sequence data. The adequacy of branch lengths for standardisation of the independent contrasts was verified by examining the relationships between the absolute value of standardised independent contrasts and their standard deviation (Garland *et al.*, 1992). This allowed an evaluation of the robustness of the results of phenotypic characters with respect to both the topology of the phylogeny and the branch lengths. A transformation of branch lengths may be required if, for example, a plot of the absolute value of each standardised independent contrast against its standard deviation shows a

negative trend (Garland *et al.*, 1992). However, no significant linear or nonlinear trends were observed in the plots, indicating that the branch lengths were adequate.

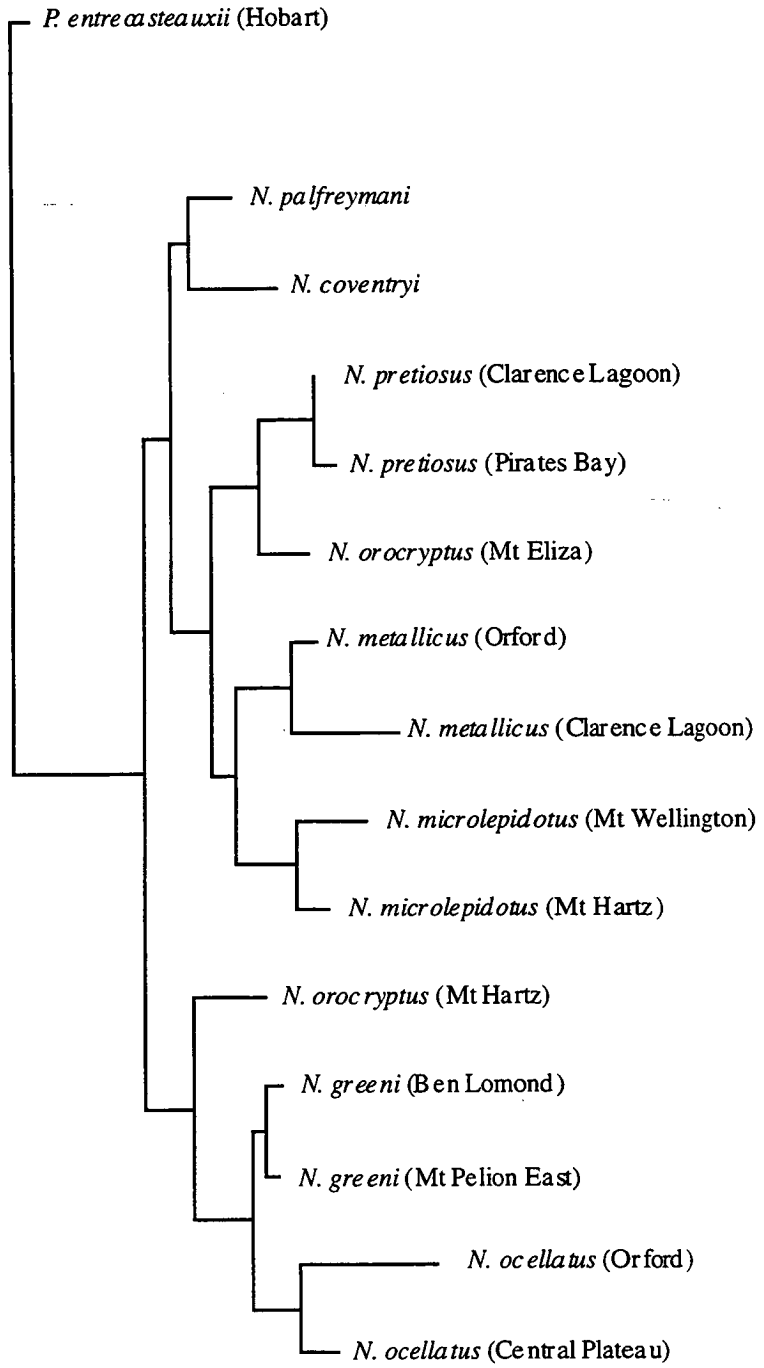


Figure 8.3 Parsimony phenogram (491 steps) to be used in comparative analysis based on 307 bp of cytochrome *b* sequence. The analysis included 8 *Niveoscincus* species and the outgroup *Pseudemoia*. TV:TI weight of 4:1.

Regardless of what "starter" branch lengths are used, independent contrasts must be adequately standardised so that they will receive equal weighting in subsequent correlation or regression analyses (see Garland *et al.*, 1992). The absolute value of each standardised independent contrast was plotted against its standard deviation, or the square root of the sum of its branch lengths. No significant linear or nonlinear trends were observed in the plots, indicating that the contrasts were adequately standardised and further transformation was not required.

A common problem in comparative studies is that the characters of interest are highly correlated with animal size (eg. Garland and Huey, 1987; Pagel and Harvey, 1988; Harvey and Pagel, 1991). One solution is to compute residuals from regressions of each character on body size and then correlate the residuals. However, there will still be the confounding effect of phylogeny (Garland *et al.*, 1992). This is easily overcome with independent contrasts. The phylogenetic analysis was run twice for the *Niveoscincus* data. Firstly, contrasts were computed with the residuals of the performance and morphological traits (having been regressed against snout-vent length) and the values of microhabitat and behaviour obtained in the field. Secondly, phylogeny was taken into account when calculating residuals. Residuals were computed using least-squares linear regression (through the origin) between the contrasts of the performance and morphological variables and the snout-vent length contrasts (both variables were log transformed before computing contrasts) to remove the effect of body length. Behaviour and microhabitat occupation were not included in this analysis as they are not directly dependent on body size, and, thus, were not regressed with snout-vent length, which was how contrasts were calculated in the second analysis.

Correlation and regression analyses were computed in SYSTAT following calculation of independent contrasts in CAIC. Reduced major-axis regression is often used in the estimate of bivariate regression slopes in independent contrast anlyses, rather than least-squares regression, as it accounts for measurement error in the independent variable (Garland *et al.*, 1992). Reduced major-axis regression is not available in

SYSTAT. Consequently, least-squares regression was used but it must be noted that this may underestimate the true slope of the data. All correlation coefficients (r), path coefficients (β) and P-values reported were obtained using phylogenetic independent contrasts. The correlation coefficients are reported as some of the correlation coefficients differed in sign to the *a priori* hypothesis.

8.3 Results

Performance abilities varied markedly between the species. The mean maximum sprint speed, for example, varied by a factor of approximately 3 (Table 8.1). There was a significant relationship between the contrasts of climb speed and jump distance in both analyses (Figures 8.4 & 8.5). Climb speed and maximum sprint speed were not significantly correlated in either analysis. However, maximum sprint speed was significantly correlated with jump distance in the first analysis (Figure 8.4) but not the second (Figure 8.5).

Phylogenetic contrasts indicated that there was a positive relationship between body size and hindlimb length ($r = 0.843$, $p < 0.001$), indicating that the larger species of *Niveoscincus* also have longer hindlimbs. Contrasts in body length explained a significant proportion of the variation in sprint speed ($r = 0.709$, $p = 0.005$) and jump distance ($r = 0.697$, $p = 0.006$). However, contrasts in body size did not account for a significant portion of the variation in climb speed ($r = -0.340$, $p = 0.234$). Relative hindlimb length, with the effects of body size removed, was strongly correlated with sprint speed, jump distance and climb speed (Figure 8.4), although the relationship between relative hindlimb length and maximum sprint speed is not as strong in the second analysis (Figure 8.5). Forelimb length also explained a significant portion of the variation in jump distance and maximum climb speed (Figure 8.5).

Table 8.1 Summary statistics for microhabitat, behaviour in the field, performance and morphological data for each population of *Niveoscincus* and *Pseudemoia entrecasteauxii* (mean ± standard error).

	Microhabitat (PCA score)	Locomotory behaviour (PCA score)	Sprint speed (m/sec)	Jump distance (cm)	Climb speed (cm/sec)	Snout-vent length (mm)	Forelimb length (mm)	Hindlimb length (mm)
N. coventryi (Mt St Leonards)	2.365 ± 0.030	-0.074 ± 0.004	0.39 ± 0.021	12.2 ± 0.35	2.6 ± 0.04	46.8 ± 1.55	11.50 ± 0.303	16.01 ± 0.475
N. greeni (Ben Lomond)	-1.134 ± 0.016	1.314 ± 0.036	0.89 ± 0.055	31.9 ± 0.72	3.0 ± 0.21	58.2 ± 1.57	19.78 ± 0.355	24.87 ± 0.388
N greeni (Mt Pelion East)	-1.176 ± 0.013	0.998 ± 0.056	0.90 ± 0.060	34.1 ± 0.80	3.1 ± 0.20	60.8 ± 3.81	20.19 ± 1.267	25.20 ± 1.461
N. metallicus (Orford)	-0.104 ± 0.056	0.022 ± 0.006	0.50 ± 0.047	15.9 ± 0.54	3.0 ± 0.06	50.9 ± 1.39	13.72 ± 0.234	18.66 ± 0.368
N. metallicus (Clarence Lagoon)	0.561 ± 0.057	-0.018 ± 0.022	0.54 ± 0.045	15.8 ± 0.73	3.2 ± 0.07	53.3 ± 1.14	14.69 ± 0.299	20.08 ± 0.472
N. microlepidotus (Mt Hartz)	-0.309 ± 0.027	-0.018 ± 0.055	0.51 ± 0.078	25.8 ± 0.94	3.0 ± 0.10	55.1 ± 1.67	18.32 ± 0.442	23.56 ± 0.558
N. microlepidotus (Mt Wellington)	-0.981 ± 0.032	0.102 ± 0.042	0.46 ± 0.043	24.4 ± 0.82	3.2 ± 0.07	55.8 ± 1.45	18.78 ± 0.385	23.95 ± 0.517
N. ocellatus (Lake Augusta)	-0.960 ± 0.025	0.771 ± 0.054	0.92 ± 0.057	38.0 ± 0.72	2.1 ± 0.13	70.9 ± 1.99	23.13 ± 0.532	29.36 ± 0.710
N. ocellatus (Orford)	-0.334 ± 0.038	0.897 ± 0.043	0.72 ± 0.052	33.6 ± 0.90	2.6 ± 0.09	58.8 ± 0.89	19.34 ± 0.265	25.03 ± 0.239
N. orocryptus (Mt Eliza)	0.708 ± 0.065	-1.715 ± 0.127	0.55 ± 0.068	18.9 ± 1.23	4.1 ± 0.33	49.0 ± 1.09	16.66 ± 0.344	21.73 ± 0.597
N. orocryptus (Mt Hartz)	-0.261 ± 0.028	0.040 ± 0.038	0.67 ± 0.032	25.5 ± 0.94	3.0 ± 0.07	55.2 ± 2.26	16.64 ± 0.47	21.88 ± 0.491
N. pretiosus (Clarence Lagoon)	0.937 ± 0.022	-1.583 ± 0.088	0.45 ± 0.027	18.9 ± 0.76	4.6 ± 0.48	47.2 ± 1.06	15.88 ± 0.379	20.13 ± 0.605
N. pretiosus (Pirates Bay)	1.254 ± 0.048	-1.402 ± 0.073	0.48 ± 0.032	16.1 ± 0.54	4.2 ± 0.36	47.9 ± 1.56	16.08 ± 0.315	20.46 ± 0.489
P. entrecasteauxii (Hobart)	0.504 ± 0.043	-0.062 ± 0.001	0.35 ± 0.028	10.1 ± 0.62	2.5 ± 0.05	46.7 ± 1.60	10.54 ± 0.321	15.25 ± 0.423

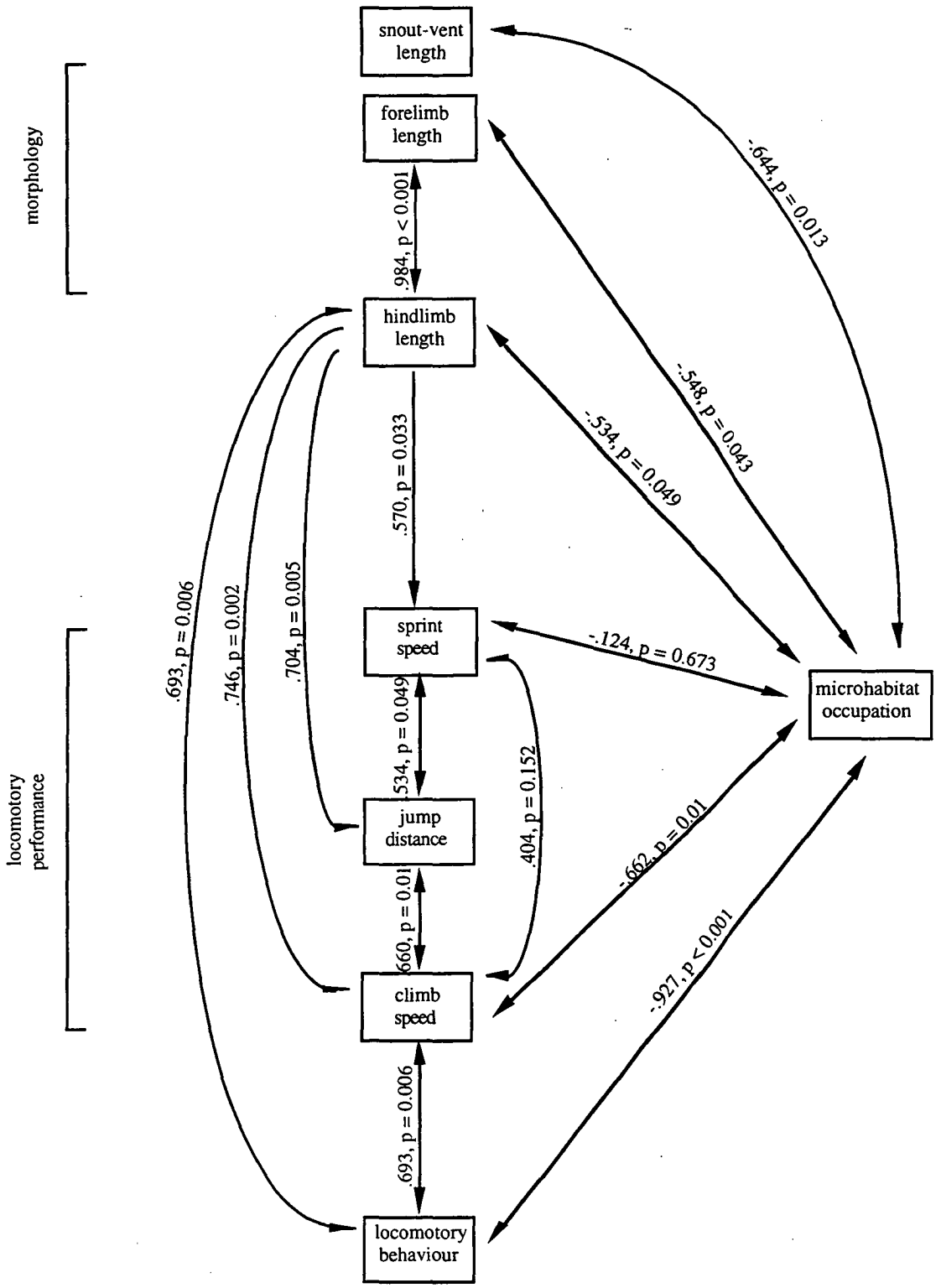


Figure 8.4 Path diagram of the evolutionary relationships between phenotypic traits, based on independent contrasts. Double ended arrows indicate correlations and single ended arrows regressions. The numbers above the lines refer to path coefficents and probability values for correlations or standardised partial regression coefficients and probability values for regressions.

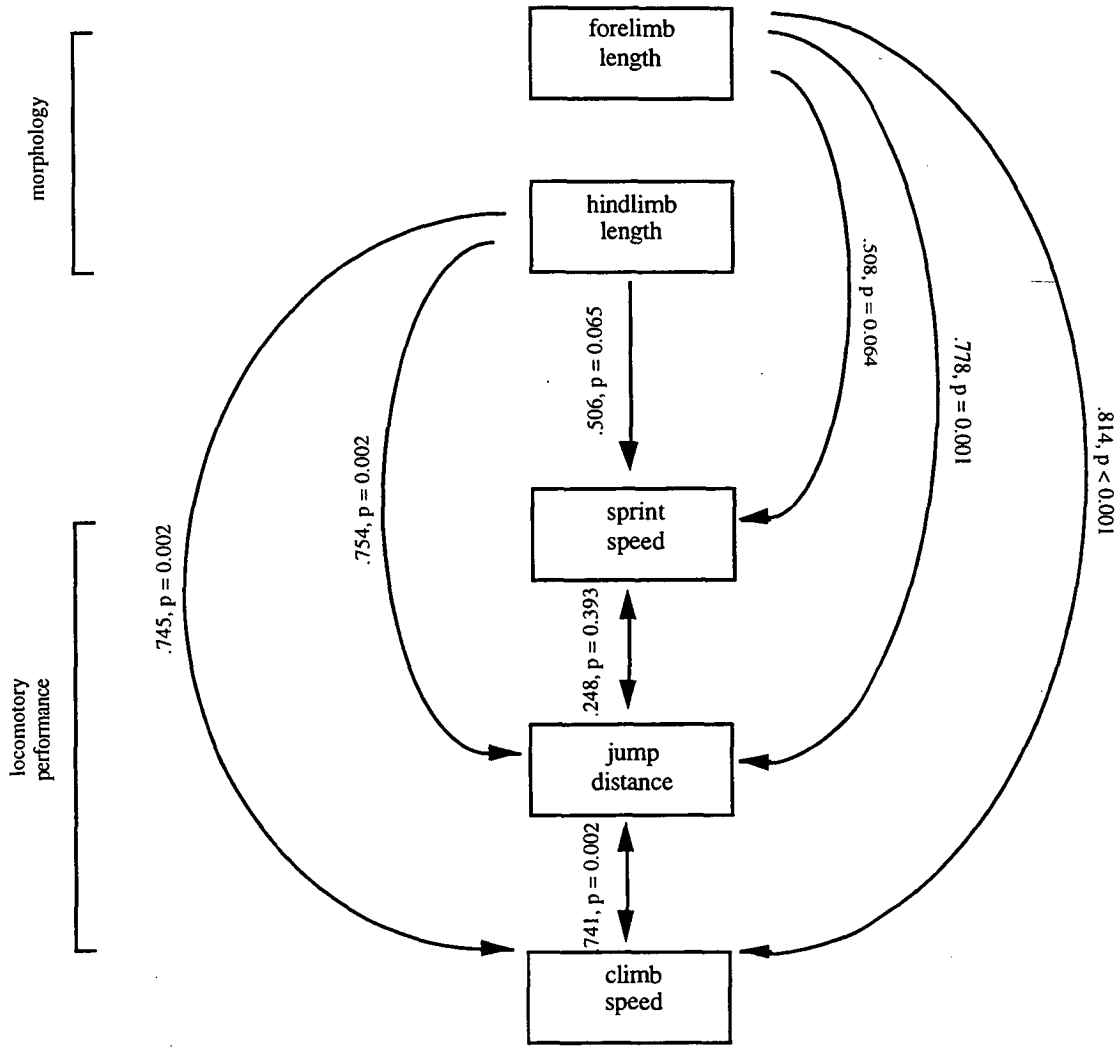


Figure 8.5 Path diagram of the evolutionary relationships between morphological and performance traits, based on independent contrasts. Values for regression and correlations were computed using a least-squares linear regression (through the origin) between the contrasts of the variable and the snout-vent length contrasts (both variables were log transformed before computing the contrasts) to remove the effect of body length on the characters. Double ended arrows indicate correlations and single ended arrows regressions. The numbers above the lines refer to path coefficients and probability values for correlations or standardised partial regression coefficients and probability values for regressions.

A multiple regression analysis of the raw data for the residual hind limb length, microhabitat use and maximum sprint speed (Figure 8.6) indicated that species occupying open microhabitats, characterised by long relative hindlimbs, had a high maximum sprint speed. There was a different relationship when sprint speed was replaced by climb speed (Figure 8.7). This multiple regression indicated a positive relationship in which species occupying closed microhabitats, with long relative hindlimb length, had a high maximum climb speed. The path coefficients indicated that

there was a significant relationship between microhabitat occupation and climb speed and the morphological traits measured (Figure 8.4). However, there was no significant relationship between microhabitat occupation and sprint speed or jump distance.

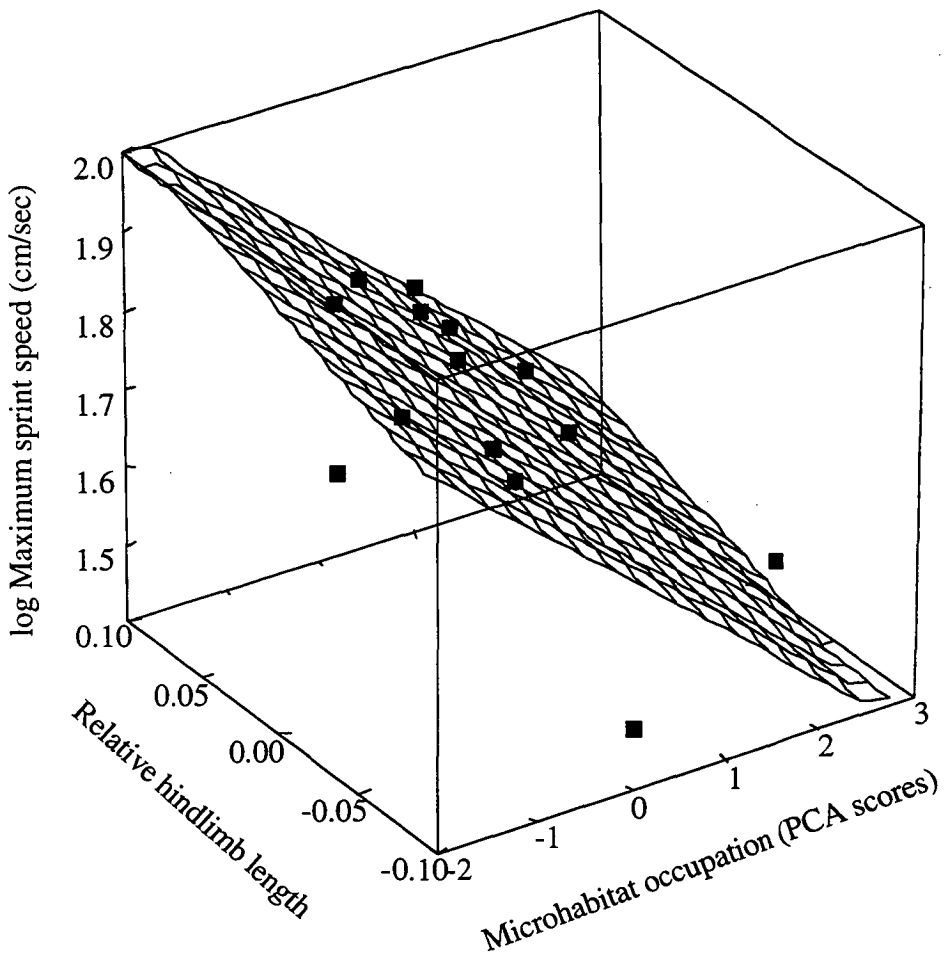


Figure 8.6 Multiple regression plane of the scatterplot of the relationship between maximum sprint speed, relative hindlimb length and microhabitat occupation. Values used are from the raw species data, not independent contrasts.

There was a stong negative relationship between microhabitat occupation and behaviour in the field (Figure 8.4). This indicates that species occupying an open microhabitat tend to jump while moving, while species occupying a more closed microhabitat have a tendency to climb. Behaviour in the field was also strongly correlated with climb speed: lizards which climb in the field had high maximum climb speeds. Relative hindlimb length was positively related to behaviour in the field (Figure 8.4), indicating that lizards that climb in the field have longer legs.

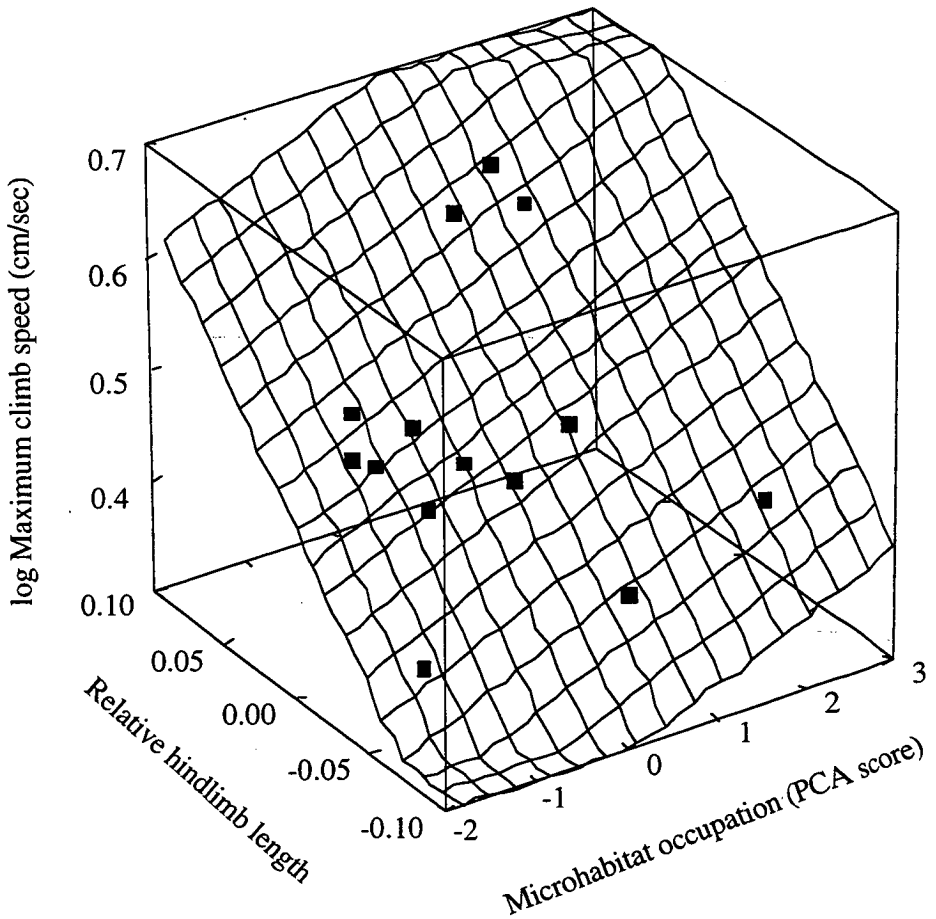


Figure 8.7 Multiple regression plane of the scatterplot of the relationship between maximum climb speed, relative hindlimb length and microhabitat occupation. Values used are from the raw species data, not independent contrasts.

8.4 Discussion

8.4.1 The relationship between morphology and performance capabilities

Performance testing is a crucial step towards understanding the ecological and fitness consequences of morphological variation (Wainwright, 1994). However, when attempting to measure the correlation between morphology and performance there is a danger of finding spurious correlations as so many morphological features tend to covary. For example, large lizards are usually found to run faster than small lizards but which of the many functional features that change with body size are responsible for

this phenomenon? My study incorporated a simple biomechanical analysis using video footage (see Chapter 6) of sprinting and jumping, to help generate specific predictions about how variation in particular morphological features will influence peformance capacity. In both performance traits it was evident that it was the hindlimbs that provided the propulsive force of movement.

Biomechanical models predict that hindlimb length, through its effect on stride length, should be a major determinant of maximum sprint speed (Garland, 1983; Garland and Losos, 1994). A positive relationship betwen relative hindlimb length and running speed has often been postulated as the mechanistic link relating differences in limb proportions to differences in behaviour and/or ecology (Garland and Losos, 1994). Therefore, larger species with longer limbs, or species with long limbs relative to body length, should run faster than smaller species or those with relatively short legs. However, only a few studies have provided evidence supporting this assumption (eg. Losos, 1990; Bauwens *et al.*, 1995). Bauwens *et al.* (1995) reported that correlated evolution of maximum sprint speed, morphology and thermoregulatory behaviour exists in 13 species and subspecies of lacertid lizards. Miles (1994) found that a transition from terrestriality to rock dwelling was accompanied by a morphological shift in the Phrynosomatidae. The only common morphological change was body size, the saxicolous descendant species being larger than the terrestrial ancestor. A similar situation exists in *Niveoscincus*. There is a positive relationship between hindlimb length, microhabitat occupation and sprint speed. Correlated evolution of leg length and sprint speed has also been demonstrated. These results support the prediction that long limbs increase the length of stride and thereby maximum sprint speed.

It was predicted in Chapter 6 that limb length would play an important factor in the ability of a lizard when jumping or climbing. Rear leg length was observed to be an important propulsive force in both activities. Similarly, the forelimbs were shown to play an important role in determining the angle of the body during jumping in Chapter 6 and were often the first point of contact in landing, thus absorbing the impact of

landing. The forelimbs were also shown to pull the lizard foward during climbing. The phylogenetic analysis in this chapter showed that limb length is strongly correlated with climb speed and jump distance in *Niveoscincus*. Consequently, limb length is an important predictor of climbing and jumping ability in *Niveoscincus*, with long-legged lizards having the potential for superior performance than short-legged lizards.

8.4.2 Correlated evolution of performance, morphology, behaviour and ecology

The phylogenetic analysis of 8 species involving 15 populations from a relatively homogenous clade of lizards indicates that the evolution of high maximum sprint speed, long jump distance and fast climbing is mechanistically related to the evolution of longer hindlimbs (relative to body length). The correlated evolution of traits related to performance has resulted in the arrangement of the extant species along a continuum of low to high performance levels. There also appears to have been a bifurcation of high climbing abilities and high sprinting/jumping abilities in *Niveoscincus* in the past, in which *N. greeni, N. ocellatus* and *N. orocryptus* (Mt Hartz) diverged from the other species to become those with the high sprinting/jumping abilities. These evolutionary patterns may be the result of different directional selection pressures in different lineages. For example, it is possible that the historical "fitness gradient" for high climb speed differed in the lineages of the extant species studied. A number of questions, discussed below, are raised by this possibility. What factors may have resulted in such a phylogenetically variable history of natural selection? Why are some species characterised by low performance abilities? Why is long hindlimb length positively related to all performance abilities, yet none of the species with relatively long legs were found to have high abilities in all performance traits?

Performance, microhabitat occupation and morphology

Much has been written concerning the general relationship between morphology and the environment (see Ricklefs and Miles, 1994). A cornerstone of the nature of organismal diversity is the notion that phenotypic differences between individuals or

species are related to differences in their ecology (Wainwright, 1994). Correlations of morphological structures with ecology and behaviour emphasise the intimate link between phenotype and the environment. One aspect of ecomorphological analysis has been the concentration on the adaptive nature of phenotype and how particular phenotypes maximise fitness in particular environments. This has been examined in studies of survival and reproductive success of alternative phenotypes (Endler, 1986), as well as by analysing the function of certain structures (Lauder, 1990; Wainwright, 1991), or by the extrapolation of laboratory measurements of mechanical and physiological capabilities to natural settings (eg. Wainwright, 1987; Sinervo, 1990; Wainwright *et al.*, 1991).

An individual's phenotype will determine the limits of its performance as the ability to perform many behaviours is rooted in the design of underlying functional systems (Wainwright, 1994). For example, the design of locomotor systems places limits on sprint speed. Performance capacity in turn affects ecology in two major ways. Firstly, limitations on performance will constrain the range of environmental resources that individuals can exploit. Secondly, the performance ability of an individual will also affect its fitness in a particular environment. For example, the performance capabilities of an individual may influence patterns of resource use, which will directly affect fitness (Wainwright, 1994).

It has previously be suggested that selection for high sprint speed is likely to be most intense in species that live in habitats that are sparsely vegetated, have high levels of predation or contain fast moving prey types (Bauwens *et al.*, 1996). This chapter has shown that there is a relationship between sprinting or jumping ability, hindlimb length, and the openness of the microhabitat occupied by a species. Species of *Niveoscincus* occupying open, sparsely vegetated habitats in Tasmania (eg. *N. greeni, N. ocellatus*) would probably be advantaged by high sprinting and jumping abilities. These habitats tend to be the large glacial boulder fields, common in many alpine habitats, and jumping, for example, would greatly increase the speed at which a lizard

could move through this environment. A lizard is likely to move much faster by jumping from one rock to another than by moving up and down the face of each rock. Selection for high sprint speed and long jump distance is likely to confer advantages in foraging, predator escape, and energy expenditure. This should result in the evolution of those morphological traits, such as long hindlimbs, that enable lizards to attain these attributes.

The attainment of high speed is probably less important for lizards that inhabit sites with dense vegetation. In these habitats greater shelter from predation, fewer predators or slow moving prey may result in weak selection pressure for high sprint speed (Bauwens *et al.*, 1996). A relaxed selection regime for sprint speed should allow relatively independent evolution and divergence of the morphological traits that affect sprint speed. Long hindlimbs may even hinder movement on the ground in dense vegetation. In such circumstances the evolution of long hindlimbs and hence high sprinting abilities may be constrained. My study has shown that those species that occupy densely vegetated microhabtiats on the ground have short hindlimbs and poor sprinting ability (*N. metallicus, N. coventryi* and *P. entrecasteauxii*). In Chapter 7, it was found that *N. metallicus*, the most widely distributed ground-dwelling species, actually had a slightly longer relative humerus than other species, possibly adding strength to the forelimbs. This species may be able to move faster through its environment by pulling itself with its forelimbs than by propelling itself with long hindlimbs. This suggests that selection pressure for high sprint speed in the ground dwelling species of *Niveoscincus* may be very weak.

Performance, morphology, microhabitat occupation and behaviour

This study has shown that long hindlimb length is positively related to all performance abilities, yet none of the species with relatively long legs were found to have high abilities in all performance traits measured. This is possibly a result of the evolution of different behavioural traits between the species. It has been a common idea that behavioural shifts precede morphological or physiological change (Huey and

Bennett, 1987). It has also been proposed that the effects of behaviour and morphology on performance are similar, although varying in magnitude (eg. Bock, 1970; Caple *et al.*, 1983). The relationships between morphology, microhabitat occupation and locomotor behaviour are consequently complex. For example, Emerson and Koehl (1990) found that derived morphological and postural features in "flying" frogs do not necessarily change a suite of performance variables in the same way and that the performance consequences of postural shifts are a function of morphology. They concluded that this showed that the potential complexity of morphological and behavioural interactions in the evolution of new adaptive types is much greater than previously considered. Moermond (1979a,b) attempted to unravel some of these relationships with the habitat matrix model, which predicts that both morphology and behaviour reflect interspecific differences in microhabitat occupation. The model predicts that lizards will jump more often when available structures are nearby. On broader surfaces running will be used more often, while narrow surfaces will result in slower progression. These hypotheses have rarely been tested.

A number of species of *Niveoscincus* seem to have specialised behaviourally, increasing their potential fitness in a particular microhabitat. Arboreal species would be advantaged by good climbing and clinging ability, making them surefooted high above the ground. Consequently, a lizard which has a behavioural tendency to jump off a surface, rather than to climb, such as *N. greeni* (see Chapter 6), may have a reduced fitness in an arboreal niche, as jumping off a branch may cause injury. Arboreal lizards, such as *N. pretiosus*, may have a reduced fitness in an open boulder field, as their aversion to jumping (see Chapter 6) may result in reduced locomotory effectiveness. Movement through a rocky environment would be very slow and possibly energetically inefficient if a lizard only walked or ran.

Evolutionary specialisation to a particular niche may come at the expense of lowered fitness in other niches (Huey and Hertz, 1984). A trade-off between different behavioural traits may exist in *Niveoscincus*. It appears that *N. pretiosus* is

behaviourally specialised for an arboreal habitat, while *N. greeni* is specialised behaviourally for an open, rocky microhabitat. However, other species of *Niveoscincus* appear to be behavioural generalists. These are the species which occupy both the boulder fields and heathlands in alpine and subalpine areas. For example, *N. microlepidotus* both climbs and jumps in the field and has been shown to have moderate performance ability at sprinting, jumping and climbing, with excellence in none of the locomotor behaviours investigated. This suggests that the behavioural traits of a lizard may directly affect its fitness, as is predicted by Arnold's (1983) paradigm (Figure 8.1). The behavioural trade-offs involved in specialising in jumping, sprinting or climbing in *Niveoscincus* are summarised as a flow model in Figure 8.8.

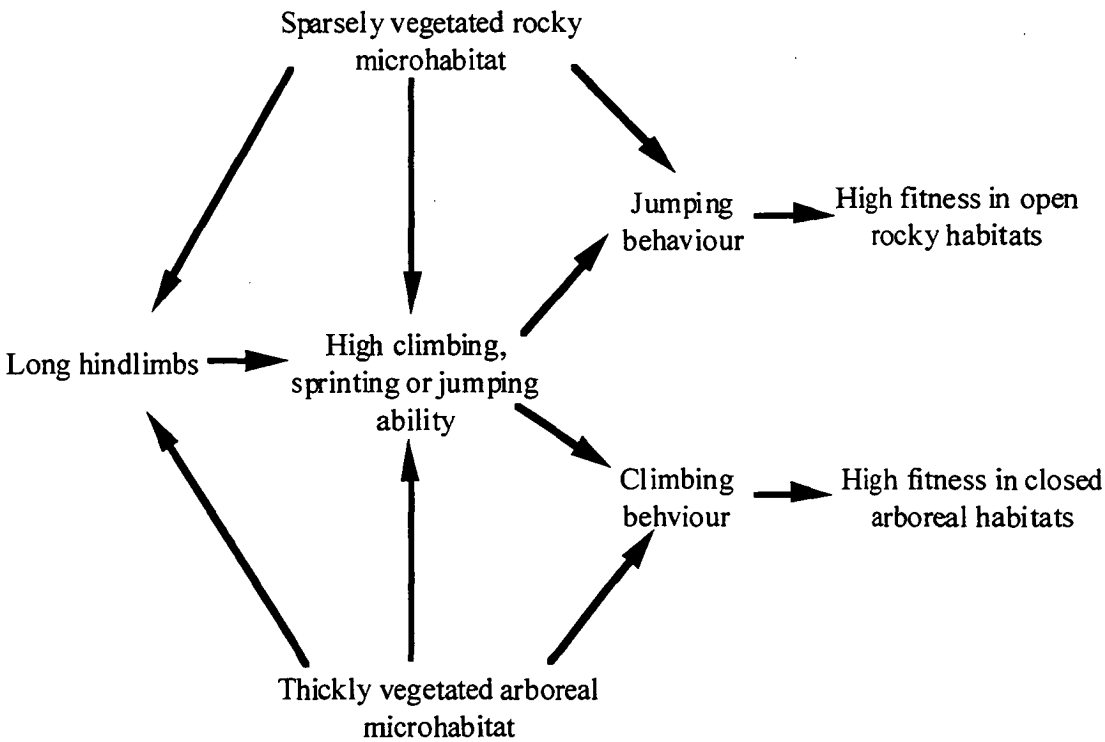


Figure 8.8 Extrapolation of Arnold's (1983) paradigm to show the proposed role of long hindlimbs in *Niveoscincus*. The behaviour of a lizard ultimately affects its fitness in a particular microhabitat.

In evaluating this model a number of factors need to be considered before it can be assumed that behavioural traits are the most significant evolutionary factors distinguishing saxicolous species from arboreal species. Firstly, the species of *Niveoscincus* may not have reached their evolutionary optimum at the time of this

study. The species may still be in the process of adaptive radiation and greater morphological and behavioural differences between the species may exist in the future.

Secondly, this study used total leg length as the only morphological feature which distinguished performance abilities. Body size was found to vary with microhabitat occupation; larger species tended to be saxicolous and body size was found to be related to performance ability. Thus, body size may have played an important role in the evolution of saxicolous and arboreal species in *Niveoscincus*. However, other morphological characteristics could also be important, such as dry adhesion in climbing lizards. Dry adhesion results from the intermolecular forces between the substrate and the microscopic setal hairs found on lamellar scales (Losos, 1990). An increase in lamella number should enhance the ability of a lizard to cling to a rough surface. Anolid lizards with many subdigital lamellae use narrower perches than those with fewer lamellae (Losos, 1990). Similarly, *Pransinohaema virens*, an arboreal skink, differs from its closest relatives in that it exhibits subdigital adhesive setae. These setae are similar to those found in some species of *Anolis* in shape and are similar in size to the subdigital lamellae of many geckos. The other species of *Pransinohaema* have pad scales which are folded and ruffled. Consequently, there are two lineages of epidermal specialisation within this small radiation (Williams and Peterson, 1982). Thus, the evolution of morphological traits other than leg length may be important determinants of performance abilities in *Niveoscincus*. The importance of other morphological traits needs to be examined to further clarify the complex relationships between performance, microhabitat, behaviour and morphology.

Evolutionary mechanisms

The observed trait combination described in *Niveoscincus* may have evolved in response to correlated selection pressures. Thus, the set of co-evolved features could be considered a phenotypic analogy to a co-adapted gene complex (Huey and Bennett, 1987; Bauwens *et al.*, 1996). Co-adaptation seems to have involved multiple levels of biological organisation (eg. morphology, physiology and behaviour).

The pattern of interspecific character covariation described in this chapter may also be a result of genetic correlations among the traits studied. For example, traits related because of straightforward biomechanical or physiological interactions (eg. relative hindlimb length and maximum sprint speed) should also tend to show significant genetic correlations. Selection forces or even genetic drift may affect only one trait but because of genetic links a whole suite of phenotypic characteristics might be affected. Thus, genetic links may cause correlated evolution in the direction indicated by the genetic correlation (eg. Emerson and Arnold, 1989; Garland and Losos, 1994; Bauwens *et al.*, 1996).

The hypothesis of correlated selection pressures is suggested for traits not genetically correlated. There is no quantitative genetic data available for *Niveoscincus* for the traits studied. Logically a number of the traits may have genetic links if biomechanical models are considered. For example, a genetic correlation between hindlimb length and sprint speed may exist. Thus, a quantitative genetic analysis to examine genetic correlations in a number of the traits studied in this chapter would help determine whether evolution in this genus is a result of genetic correlations or selection pressures.

CHAPTER 9 GENERAL DISCUSSION

9.1 Overview of this thesis

Ecological morphology is broadly concerned with making connections between how organisms are constructed and the ecological and evolutionary consequences of that design (Reilly and Wainwright, 1994). Consequently, the primary theme of this thesis has been to integrate the five research axes (phylogeny, performance, morphology, behaviour and microhabitat occupation) to achieve a deeper understanding of the ecological and evolutionary basis of locomotory abilities in *Niveoscincus*. It has examined the effect behaviour and morphology has on determining how an organism interacts with its environment. This has been a multidimensional task and has required the integration of concepts and methods that have traditionally been distinct.

This thesis provides the only quantitative description of microhabitat occupation by all except one of the *Niveoscincus* species. The separation of microhabitat occupation between these species was also characterised. Microhabitat use by *N. metallicus* and *N. microlepidotus* has previously been investigated at a sub-alpine site on Mt Wellington (Melville and Swain, 1997a) but existing descriptions of the other species have been very generalised, providing only broad habitat preferences (Hutchinson *et al.*, 1989; Rawlinson, 1974). All the species studied here exhibited a non random selection of microhabitats and a preference for a particular set of environmental and structural factors. Microhabitat selection was shown to be strongly related to vegetation and substrate characteristics.

Locomotory behaviour has been shown to be a very important factor associated with microhabitat occupation, morphology and foraging success (Garland and Losos, 1994). Consequently, locomotor behaviour is a critical component of a lizard's life history (Pietruszka, 1986), but it has not been considered in many studies (Garland and Losos, 1994). For this reason I chose to conduct my study of locomotory behaviour in

Niveoscincus in the field. Consequently, the work reported in Chapter 5 was undertaken in order to quantify the locomotory behaviour of the study animals through multivariate analysis. The results showed that there are significant differences between the three basic ecomorph-types (ground-dwelling, arboreal and saxicolous) in *Niveoscincus* in terms of locomotory behaviour. It is also possible to divide the saxicolous group into two ecomorph types according to their locomotory behaviour: the saxicolous species *N. greeni* is significantly different from the heath/rock-dwelling species *N. microlepidotus* and *N. orocryptus* (Mt Hartz).

Arnold (1983) described performance as a measurement of an ecologically relevant activity, such as running speed. Chapter 6 investigated a number of such activities in the species of *Niveoscincus* available for study and *Pseudemoia entrecastreauxii*: sprint speed, jumping and climbing. Significant differences were found in the performance abilities of the three ecomorph-types. The saxicolous species had high sprinting and jumping abilities, while the arboreal species were shown to be fast climbers.

Other studies have found that morphological characteristics affect performance abilities in lizards. The radiation of morphological characteristics in *Niveoscincus* has not been investigated in detail and existing research has been restricted to taxonomic descriptions and qualitative discussion of evolutionary patterns of morphology (Hutchinson and Schwaner, 1989). This study provides the first opportunity to conduct a comparative investigation of morphological features relevant to ecology and locomotory performance and behaviour in the genus. The current study found that the hindfoot/femur (HFT/FEL) ratio in *Niveoscincus* was higher in the faster running species, such as *N. greeni, N. ocellatus* (Lake Augusta) and *N. orocryptus* (Mt Hartz). The arboreal species of *Niveoscincus* were shown to be lizards with short bodies and relatively long rear legs, which could be attributed to a relatively long femur.

This study provides a rare attempt to quantitatively estimate the relationships among measurements of an ecologically relevant performance capability and different

morphological, habitat and behavioural traits within a group of closely related organisms. It addressed a number of important issues in ecomorphology: (1) the interspecific relationship between morphology and a number of performance traits in *Niveoscincus*; (2) the possible trade-off between different modes of locomotion; and (3) the co-evolution of performance, morphology, behaviour, and microhabitat occupation.

9.2 Conclusions

A historical comparative method clearly has a great deal to offer in ecomorphology. Much of ecomorphology examines how organisms have evolved in response to environmental circumstances. Some taxa may evolve readily and rapidly enough that historical effects will be minor, but in many cases, the key to understanding present character traits will be an understanding of the sequence, timing and cause of past evolutionary events in the past (Losos and Miles, 1994). Thus, the historical component of the study is extremely important.

A key concept in this study has been the importance of performance as a mechanistic link between morphology and the ecological and evolutionary consequences of morphology. Arnold (1983) popularised this concept and also connected this idea to experimental paradigms in quantitative genetics and ecology. Performance is an essential factor in the ability of an individual to perform ecologically relevant tasks. An individual's performance capacity places fundamental limits on the range of possible activities and ultimately the resources that can be obtained (Reilly and Wainwright, 1994). Thus, it has become a central component of research programmes that seek a causal connection between morphology and ecological patterns.

Biologists often attribute ecomorphological associations to the process of adaptation (Garland and Losos, 1994). However, many studies have shown that

ecomorphological associations may be affected by a variety of other factors. Phenotypic and environmental plasticity illustrate the bidirectional nature of the factors examined in this study. A given genotype can produce different phenotypes in response to environmental cues. Thus, the variation recorded in this study may be due to genetic differences or enviromental influences on development. This illustrates the need to distinguish between the effects of variation in genotype and the variation in environmental effects on a common genotype. This would require the incorporation of developmental plasticity into evolutionary theory, and the integration of physiology, development and the evolution of plasticity. However, one advantage of studies such as this, which seeks to integrate multiple levels of analysis, is that it allows prediction with understanding. In the ideal study one could determine the functions of specific morphological traits in performing some ecologically relevant task, measure maximal performance in the laboratory and realised performance in nature, then demonstrate how ecological variation in realised performance relates to survival and fitness of individuals in a population over time. The study could then track the functional significance of morphological traits to the ecological importance of performance on fitness. To date no study has implemented such a comprehensive integration of all levels of ecomorphology. Although this study did not examine the fitness and survival of indiviuals of a population, it did examine behavioural characteristics of animals in the field. Despite the fact that the behaviour of an animal can directly affect its fitness, this has rarely been incorporated into ecomorphological studies.

Potential trade-offs and constraints are of major concern in evolutionary biology, behavioural ecology and comparative morphology (see Garland and Losos, 1994). Constraints may prevent taxa from optimising several performance abilities simultaneously. At the commencement of this study it was hypothesised that *Niveoscincus* may show a trade-off between performance abilities as a result of morphological deifferences. This had previously been found to be the case in *Anolis*, in which lizards climbing on small twigs have short legs while species which jump from perch to perch have long legs (Losos 1990a). Consequently, anoles are not able to

utilise narrow structures and still be able to make long jumps between perches. This was not found to be the case in *Niveoscincus*, but performance work did show that there was a trade-off between sprinting/jumping and climbing. Species which climbed rapidly were not able to jump long distances or sprint quickly. The phylogenetic analysis indicated that this was not a result of differences in relative leg length; rather it was a result of behavioural factors. This study has helped indicate the importance of behaviour in the ecomorphological paradigm developed by Arnold (1983).

Of the many approaches that one might use to study animal behaviour, the comparative phylogenetic analysis has been one of the least used (Lauder and Reilly, 1996). In the past behaviour has been viewed as too variable to be reliably used to create, for example, phylogenies, but recently interest has increased in incorporating behaviour into comparative studies of evolution (Lauder and Reilly, 1996). A number of suggestions have been made in the last decade concerning the role behaviour plays in evolutionary processes. It has been a common idea that behavioural shift precedes morphological or physiological change, as changes in behaviour will directly affect an animal's fitness (Huey and Bennett, 1987). Until recently there has not been any strong evidence to support this assertion, but a phylogenetic study, which examined morphological characteristics and behaviour of sand-diving in Laelolaemus (Halloy, pers. comm.), has shown that the behavioural shifts probably occurred prior to morphological changes. Similarly, my study has shown that behavioural specialisation for particular microhabitats has probably occurred prior to morphological changes. It is possible that this study has taken a "snapshot" of *Niveoscincus* in the process of diversification or even that high levels of morphological specialisation are not appropriate in this genus. As was discussed in Chapter 3, the climate and, consequently, the vegetation of Tasmania has been highly variable over the past million years. It is possible that it has been of greater advantage for the *Niveoscincus* species not to have highly specialised body shapes, allowing them to survive in a range of different microhabitats in an unstable and changing environment.

CHAPTER TEN

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